Relationships Between Foraminifera and Geomorphology: Holocene, Crooked-Acklins Platform, Southern Bahamas

By

Maritha E. Huber

Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Science.

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Chair: Dr. Eugene C. Rankey

_____

Dr. Evan K. Franseen

_____

Dr. Alison Olcott-Marshall

Date Defended: 07/19/2016

The Thesis Committee for Maritha E. Huber

certifies that this is the approved version of the following thesis:

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Chair: Dr. Eugene C. Rankey

Date approved: 07/22/2016

Abstract

Although general ecologic controls on the occurrence, growth and shape of foraminifera are well understood, the spatial patterns of foraminiferal distribution across carbonate isolated platforms and their relationship to geomorphic setting are not well constrained. To provide a tool for constraining and predicting spatial variability in ancient analogs, this study tests the hypothesis that ***foraminiferal populations vary among geomorphic settings*** by studying Holocene sediment of Crooked-Acklins Platform, southern Bahamas, by foraminiferal population analysis (including the abundance and diversity of foraminiferal genera). To test the hypothesis, this study integrates observations of remote sensing data, bottom type, epifauna, grain sizes, and foraminiferal populations.

Results reveal that foraminiferal abundances, diversity and assemblages vary systematically across the isolated carbonate platform. On this platform, twenty-two foraminiferal genera include generalists (genera present across the platform; e.g., *Archaias*, *Peneroples* and *Quinqueloculina*) and specialists (genera that are spatially restricted; e.g. *Clavulina*, *Rosalina* and *Homotrema*). The abundances of these foraminifera, and the diversity and evenness of associations in surficial sediment in, the geomorphic are greater in geomorphic elements near the open ocean (back-reef shelf, southern unrimmed shelf and southern part of the shoal). In contrast, geomorphic elements further from the margin (northern part of the shoal part of the shoal, platform interior and tidal flat) have generally low diversity, evenness and foraminiferal abundance. The distribution patterns and abundances of the 22 distinct genera suggests that not all geomorphic elements are uniquely defined by one foraminiferal assemblage – some geomorphic elements include more than one assemblage, and some assemblages extend across two or more geomorphic elements. Similarly, foraminiferal distribution trends in shallow Holocene sediment cores reveals patterns that the mimics the distribution of the surface sediment, although details appear altered by taphonomic changes from bioturbation and

rhizoturbation. The results suggest that coupled sedimentologic and foraminiferal characterization provide the most accurate interpretation.

Integrated sedimentologic observations, foraminiferal patterns, and previous studies provide a basis for a conceptual model for controls on foraminiferal distribution. This conceptual model could be applied to ancient systems to understand and predict depositional variability related to distinct geomorphic and depositional settings.

Acknowledgements

This study was funded by the Kansas Interdisciplinary Carbonate Consortium (KICC) and the Geology Department of the University of Kansas. First I would like to thank my advisor, Dr. Gene Rankey. Throughout the past 3 years, he has supported me and pushed me to grow as a researcher and as a person. I would also like to thank my committee members, Dr. Evan Franseen and Dr. Alison Olcott-Marshall, for their time and effort during the writing process and their comments and support throughout the three years of my graduate career.

Additionally, thanks to the people of the Bahamas and the Department of Marine Resources who granted the research permit. Special thanks to Dennis Thomson for his time and help during field work. Also, special thanks to Alexa Goers, Steven Herbst, Abdul Wahab and Dr. Steve Hasiotis for their help during field work. Jennifer Lowery, Tom Neal, Michelle Mary, Paul Seldon and Jennifer Roberts helped me during the lab work phase of my thesis. Additionally, I would like to thank Geoff Boeing for his time during the data analysis phase of my thesis.

Finally, a very special thank you to all people who have supported me during these three years of my life. No words describe how thankful I am for you. This very large group includes the KU Catering staff, especially, Robert Pierrelee, Ellen Green, Pat Rap, Elisa Brown and Dan Palin. Thanks also to Brant Konetchy, Isabel Villaneda-Vanvloten, Richard Bell, Allison Joy, Michelle Mary, Tom Neal, Adrianne Duarte, Steven Herbst, Alexa Goers, Robert Rader, James Lamsdell and James Golab. Additionally, I like to thank my family for all the support they have given me throughout my life.

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Introduction

Many ancient carbonates represent deposition on isolated platforms, and include a range of sediment of distinct character that initially accumulated within different geomorphic elements (mappable depositional or erosional bodies of the seascape with distinct relief or bathymetry) (e.g. Eberli et al., 1993; Wilson and Evans, 2002; Wilson and Vecsei, 2005). These geomorphic elements commonly are associated with variable energy levels, salinity, and turbidity, environmental factors that may also influence biota that produce the sediment (Ginsburg and Lowenstam, 1958; Hallock and Glenn, 1986; Murray, 1991; Pomar, 2001; Beavington-Penney and Racey, 2004).

Benthic foraminifera are important carbonate sediment producers in warm, shallow marine settings preserved in strata of Cambrian to recent age (Hallock, 1981; Loeblich and Tappan, 1988a). As they are sensitive to environmental conditions, shallow marine foraminifera can be important tools for paleoenvironmental interpretation and facies analysis of carbonate successions (Hallock and Glenn, 1986; Jordan and Abdullah, 1988; Murray, 1991; Scheibner et al., 2003; Mohamed et al 2014). Although numerous studies have examined spatial patterns of foraminiferal distribution (e.g. Lie et al., 1997; Hohenegger, 2001; Hallock et al., 1986; Renema, 2006; Parker and Gischler, 2015), few studies have characterized spatial linkages between geomorphic elements and foraminiferal distribution explicitly.

To explore potential utility of foraminifera for identification of geomorphic elements in geologic analogs, this study tests the hypothesis that ***foraminiferal populations vary with geomorphic elements*** by examining Holocene sediment of Crooked-Acklins Platform, southern Bahamas. To better understand the linkage between geomorphic elements and foraminiferal assemblages, this study integrates observations of remote sensing data, geomorphic element, bottom type, grain size, and foraminiferal genera abundance and diversity in surface sediment and shallow sediment cores. The results of this study provide a generalized conceptual model that may be applied, through the principle of taxonomic uniformitarianism (Beavington-Penney

and Racey, 2004; van Gorsel et al., 2014), to understand and predict facies bodies in ancient isolated platform analogs, including Miocene platforms in south eastern Asia and the Tethys region (e.g. Jordan and Abdullah, 1988; Eberli et al., 1993; Geel, 2000; Fournier et al., 2004).

Regional setting and platform geomorphology

Crooked-Acklins Platform (CAP), located in the southern Bahamas (Fig. 1), covers about 2600 km^2 and is located between 22° and 23°N (Rankey and Reeder, 2010). Like many Bahamian platforms, CAP includes a range of geomorphic elements (e.g., shoal, tidal flat, platform interior, shelf, back-reef shelf). The north-facing margin extends for almost 50 km along strike, and includes one of the longer barrier reefs of the Bahamas. This reef is flanked by a 1-3 km wide back-reef shelf that extends south to Crooked Island (Fig. 1). Islands (Crooked, Acklins, and Long Cay) ring the platform on three sides, protecting a broad platform interior. The south sides of Crooked and western Acklins islands (Fig. 1) transition into a broad (up to 1-2 km wide) tidal flat complex (Berkeley and Rankey, 2012) (Fig. 1). The tidal flat complex passes southward into the subtidal platform interior, connected to the open ocean by an inlet between Crooked Island and Long Cay and the more open southwestern margin (Fig. 1). The tidal inlet (known as French Wells) hosts an ebb delta (Rankey and Reeder, 2010; Rankey, 2014). The southwestern margin includes an aggraded ooid shoal complex (Rankey and Reeder, 2010; Rankey, 2014), with several small islands of Holocene age (locally known as Fish Cays) (Fig. 1). The shoal complex acts as a barrier to open-ocean wave energy, although tidal exchange occurs through channels and the broad areas to the southeast and west of the shoal complex (Fig. 1). The sandy shelf south of the shoal is unrimmed and displays some patch reefs and some areas of rocky bottom (Rankey and Reeder, 2010). These geomorphic elements display a range of different bottom types, biota and grain sizes (Table 1).

The Crooked-Acklins Platform is located in a subtropical and semi-arid climate (Pierson, 1982), with monthly mean maximum air temperatures ranging from 26 to 31 °C (Berkeley and

Rankey, 2012) and precipitation of 880 mm/yr (Pierson, 1982). CAP is located in the easterly trade wind belt, with dominant wind from the east to south-east (Berkeley and Rankey, 2012). These winds create small wind waves during the summer; during the winter, larger waves are created by storms and cold fronts, in which winds can blow from the south, west and north (Rankey and Reeder, 2010; Berkeley and Rankey, 2012). These larger waves can have significant wave heights in the platform interior of up to 0.7 m (Rankey and Reeder, 2010). CAP also is influenced by semi-diurnal tides, with an open-ocean spring tidal amplitude of ~1 m, with lower ranges into the platform interior. These tides and waves generate currents with speeds in the shoal that reach up to 0.70 m/s, less in the interior (Rankey and Reeder, 2010; Rankey, 2014).

Environmental conditions (energy, salinity, water depth, bottom types and epifauna) vary across the platform (Table 1). In general, water of normal marine salinity dominates CAP, except for the tidal flat, where hypersaline or brackish conditions can occur in response to evaporation or intense rain events. The sediment on CAP are dominantly in the medium (125-500 μm) to coarse fraction (>500μm); mud is rare except on the tidal flat (Rankey and Reeder, 2010; Berkeley and Rankey 2012).

Methods

For this study, 183 surface sediment samples were collected in field seasons between 2008 and 2014 along 12 transects (Rankey and Reeder, 2010; Berkeley and Rankey, 2012; Rankey 2014) that cover the range of geomorphic elements (interpreted initially by Rankey and Reeder, 2010). Samples collected in small plastic vials were capped at sampling depth to preserve the fine sediment fraction. At each sample location, attributes of bottom type, including visual estimation of the abundance of biota (flora and fauna), water depth, and visual estimation of sediment disturbed by burrows and physical sedimentary structures were captured. Each sample location was marked with a hand-held GPS.

Following field work, the benthic foraminifera in sediment samples were analyzed under a microscope. Because planktonic foraminifera are either sparsely present or absent on platforms (Hallock and Glenn, 1986), this study examined only benthic foraminifera, and planktonic foraminifera were not analyzed. In each sample, 300 foraminifera were picked from sediment, with no differentiation between living and dead foraminifera, to ensure statistically valid data (Gischler et al., 2003). For the two samples that did not contain 300 foraminifera, all foraminifera were analyzed and identified to the genera level. Encrusting foraminifera were included, however, since they are important on-platform carbonate producers in modern and ancient systems (Gischler and Möder, 2009; Richardson-White and Walker, 2011). The encrusting foraminifera were not differentiated, except for *Homotrema*, which represents a genus important in the Gulf of Mexico and Caribbean, where it is abundant near the platform margin, especially in reef-related sediment (e.g. Gischler et al, 2003; Gischler and Möder, 2009). Identification of foraminiferal genera was based on the standard reference of Loeblich and Tappan (1988a, b) and previous studies of shallow-water areas of the Caribbean and western Atlantic and Gulf of Mexico region (e.g. Davis, 1964; Martin and Liddell 1988; Lidz and Rose, 1989; Gischler, 2003; Gischler and Möder, 2009). These identifications form the basis for evaluation of foraminiferal abundance and diversity.

To better understand the linkage between the foraminiferal distribution and sedimentology of the CAP, grain size analysis used sieves with meshes with grid sizes of 2000µm, 1000µm, 500µm, 250µm, 125µm and 63µm; the grain sizes smaller than 63µm were caught in a bag. After the sieving, each mesh and the bag with the sediment was weighed, and the weight of the mesh (or bag) was subtracted. For some reporting, grain sizes were grouped into coarse (>500µm), medium (500µm- 63µm) and fine (<63µm) fractions.

To test conceptual models of the Holocene history of the area, foraminifera of four shallow cores were analyzed using the same methods as applied to the surface samples. Two 2.4 m long (post compaction) cores collected from the shoal complex (sedimentologically analyzed and

interpreted by Rankey, 2014) were sampled at 40 cm vertical spacing. A second set of cores from the tidal flat (sedimentologically analyzed and interpreted by Berkeley and Rankey, 2012). These tidal flat sediment cores are approximately 150 cm long (compacted) and were sampled at 20 cm spacing.

To test the hypothesis of the variation of foraminiferal populations with geomorphic elements, following identification of foraminifera, statistical methods provided a means to objectively define foraminiferal assemblages based on abundance and diversity of foraminiferal genera. This study used Q-mode cluster analysis (following the method of Gischler et al., 2003), using normalized abundance of each foraminiferal genus (in percent, defined as number of specimens of a genus divided by the total number of specimens). The analysis is based on a matrix (x = n × m) consisting of *n* samples with *m* foraminiferal genera, and groups samples into clusters based on the similarity of foraminiferal genera and their abundance. The Euclidean distances (d_{ij}; where i and j represent a pair of samples) are calculated between all possible sample pairs, as:

$$d_{ij} = \sqrt{\frac{\sum_{k=1}^{m}(x_{ik} - x_{jk})^2}{m}}$$

Here x_{ik} is the kth genus abundance measured on sample i and x_{jk} is the kth genus abundance measured in sample j. The variable k runs through all foraminiferal genera and (m). In the initial step, the two samples with the smallest distance (d_{ij}) are grouped and the new cluster Euclidean distance is computed by averaging the distance values of both samples. The clustering process is repeated until all samples form one cluster. For generating the foraminiferal assemblages, this analysis uses a 40% similarity cutoff (following Gischler and Möder, 2009). Additionally, a second Q-mode cluster analysis, following the same methodology, utilized only common foraminiferal genera (those with abundances >10%) to secure a stable assemblage result. The end result of the analysis is that samples with the similar

foraminiferal genera with similar abundances are grouped together, and samples with different genera or overlapping genera with unlike abundances form distinct groups.

To explore the differences (or similarities) among in the foraminiferal assemblages of the geomorphic elements, one-way-ANOVA analysis (following the general approach of Foreman et al., 2011) estimates the variance of the means of the foraminiferal genera abundances among the geomorphic elements. For this technique, the geomorphic elements represent the groups (*m*) and the abundances of the different foraminiferal genera are represented as the data (*n*) in the groups. In this analysis, the normalized genus abundances (defined as above) of the most common foraminiferal genera can be grouped by the geomorphic elements; only the most common genera are utilized, since the analysis does not work properly with abundant zeros in the raw data. For the one-way-ANOVA, the total sum of squares (SST) is calculated using x_{ij} as the abundance of the *ith* foraminiferal genus in the *jth* geomorphic element, with overall mean ($\bar{\bar{x}}$) and the total number of observations (N = *n* x *m*):

$$SST = \sum_{j=1}^{m}\sum_{i=1}^{n}(x_{ij} - \bar{\bar{x}})^2 = \sum_{j=1}^{m}\sum_{i=1}^{n}x_{ij}^2 - \frac{\left(\sum_{j=1}^{m}\sum_{i=1}^{n}x_{ji}\right)^2}{N}$$

Additionally, the sum of squares among the geomorphic elements (SSA) is calculated by:

$$SSA = \sum_{j=1}^{m}(\bar{X}_j - \bar{\bar{X}})^2 = \sum_{j=1}^{m}\frac{\sum_{i=1}^{n}x_{ji}{}^2}{n} - \frac{\left(\sum_{j=1}^{m}\sum_{i=1}^{n}x_{ij}\right)^2}{N}$$

Also, there may be a variance in the foraminifera within each geomorphic element. For each geomorphic element the variance is calculated as the sum of squares of the differences among each of the foraminiferal genus abundance to the mean genus abundance in the respective geomorphic element. This calculation is called the sum of squares within, or error sum of squares, and is calculated for each geomorphic element:

$$SSE = \sum_{j=1}^{m}\left(\sum_{i=1}^{n}x_{ji} - \bar{X}_j\right)^2 = \sum_{j=1}^{m}\sum_{i=1}^{n}x_{ji}^2 - \sum_{j=1}^{m}\frac{\left(\sum_{i=1}^{n}x_{ji}\right)^2}{n}$$

In general, the relationship among the three sum of squares is:

$$SSE = SST - SSA$$

To allow the calculation of the final F-test for statistical significance, the different variances (total variance, variance among geomorphic elements, and variance within geomorphic elements) is calculated using degrees of freedom. Further, the sum of squares is divided by the degrees of freedom to provide an estimate for the variance. Each category of sum of squares has a distinct degree of freedom (SST: N – 1; SSA: m -1; SSE: N – m) resulting in different variances:

$$Total\ variance = \frac{SST}{N-1}$$

$$Variance\ among\ geomorphic\ elements = MSA = \frac{SSA}{m-1}$$

$$Variance\ within\ geomorphic\ element = MSE\,\frac{SSE}{N-m}$$

Following the calculation of variance, an F-test determines the critical value for testing the significance of variance in the foraminiferal genera abundance means among the geomorphic elements.

$$F = \frac{MSA}{MSE}$$

With the critical value defined, for a given level of variance (here 0.05; a standard value for the ANOVA analysis; resulting in a 95% confidence interval) and degrees of freedom, the hypotheses can be rejected or accepted. A comparison of the values within the boundaries of the variance determines if the variance is equal, in which case the variance of each foraminiferal genus among the geomorphic elements is less than the previously set variance level of 0.05, or if the genus has a different variation, in which case the values are larger than 0.05.

To explore the foraminiferal diversity, the normalized foraminiferal genus abundance of all samples were grouped by geomorphic elements, and analyzed through use of the Shannon-Wiener diversity index (Shannon and Weaver, 1962). Created in the field of information

theory, the Shannon-Wiener diversity index is used in this study as a measure for the foraminiferal genera diversity of the foraminiferal communities, calculated by using the relative abundance of different genera and their abundance. For this study, the Shannon-Wiener diversity index is calculated for each geomorphic element. Within each geomorphic element, the total number of genera (*n*) in connection with the genera abundance (*i*) relative to the total number of genera ($p_i \ldots p_n$) are analyzed by the Shannon-Wiener diversity index, calculated as:

$$\mathrm{H} = -\sum_{i=1}^{n} p_i * \ln p_i$$

A diversity of H = 0 indicates a more homogenous community (e.g., one foraminiferal genus present), and higher H values indicate a more diverse community (with multiple genera). In geomorphic elements with *n* genera, the maximum value for H is $H_{max} = \ln n$, which would indicate a uniform abundance of foraminiferal genera. Deviation from H_{max} are described by the Shannon evenness index (E).

$$E_H = {}^{H}/_{H_{max}}$$

The Shannon evenness values, measuring of homogeneity of the foraminiferal community, range from 0 (indicating a not diverse community) to 1 (indicating a foraminiferal community with a high entropy (defined as degree of disorder or randomness in the system) in the genera distribution.

Potential errors

The study of foraminifera is associated with potential errors that can impact interpretations (e.g. Patterson and Fishbein, 1989). For example, foraminiferal genera display varying production peaks throughout the year (Hohenegger, 2006). Depending on the timing of the field work, different genera may display a higher or lower abundance than in other seasons (Hohenegger, 2006). To minimize this issue, this study examined sediment that included both living and post-

mortem foraminifera to capture the general foraminiferal community which likely accumulated over several reproduction peaks of different genera.

Additionally, organisms can burrow and disrupt sediment, causing sediment from different initial depths to mix, and foraminifera can be moved up or down the sediment column (Sevrin and Erskian, 1981). This effect can change the composition of the foraminifera. Similarly, in areas that experience a change in environmental conditions, this mixing can cause a genus characteristic of one environment to be mixed with genera from another environment. However, depending on the degree of mixing, some fraction of the original foraminiferal populations is still present. The most correct interpretation of foraminifera will emphasize the unmixed population. Foreign foraminiferal genera from another environment can be detected with a comparison with literature data. However, detecting transported foraminiferal genera that occur in throughout the burrowed section or environments is more difficult. In these situations, a comparison with literature data or a comparison with another sample of the same environment where burrowing is less prominent can help.

Beyond vertical mixing, lateral sediment transport can change the spatial distribution of foraminifera. According to Murray (1991) foraminifera need a velocity of 0.05 m/s to be transported. Additionally, according to Snyder et al. (1990) the traction velocities necessary to transport for elongated genera is between 0.06 m/s and 0.09 m/s. For elongated, coiled compressed and discoidal genera high traction velocities above 0.09 m/s are needed. Most of the foraminiferal genera in this study belong into the latter category. Previous studies (Rankey and Reeder, 2010; Rankey, 2014) illustrate that the platform interior experiences peak instantaneous orbital velocities of 0.45 m/s. Nonetheless, the most common orbital velocity measured in the platform interior CAP was 0.04 m/s, and only 10% of the orbital velocities exceeded 0.16 m/s. In the channels on the shoal complex, however, the current velocity can reach up to 0.70 m/s (Rankey and Reeder, 2010). Thus, although the majority of the waves and

currents on CAP are not strong enough to transport foraminifera, higher velocities could transport the foraminifera.

Some evidence suggests transport. Notably, some foraminifera are abraded, most commonly *Archaias*, encrusting foraminifera, *Peneroples* and *Quinqueloculina*. The three areas with an abundance of abraded tests are the back-reef shelf, the shallow subtidal northern platform interior close to the tidal flat, and the northern part of the shoal complex. In the back-reef shelf, abrasion is evident on up to 20% of *Archaias*, up to 60% of *Peneroples*, up to 15% of *Quinqueloculina* and up to 100% of encrusting foraminifera. The northern part of the platform interior has abrasion as well, with up 100% of *Archaias*, up to 45% of *Peneroples*, up to 17% of *Quinqueloculina* including evidence for abrasion. Finally, the northern part of the shoal includes abraded specimens (*Archaias* (up to 30%), *Peneroples* (up to 20%) and *Quinqueloculina* (up to 15%)). This distribution of the abraded foraminifera suggests transportation in the back-reef shelf and the northern part of the shoal. It is unclear, however, how much is due to bioturbation, oscillatory motion (e.g., by waves), or directional transport. If transported, transition zones (applied from Murray, 1991) of foraminiferal genera abundances would be expected to be gradual between populations (either due to transportation or due to transitioning environmental conditions allowing a gradual change in abundance from one population to the other).

In sum, the current and wave velocities on CAP suggest that only high energy events have the potential to transport foraminifera, whereas the majority of the measured velocities are too low for transportation. The abraded foraminiferal specimens suggests that there is some transport, and transportation of foraminifera cannot be ruled out as an influence on distribution of genera. Nonetheless, as energy (and transportability) is a function of environment, its influence is implicitly included in mapping distribution patterns.

Results – Patterns of foraminiferal distribution

Types and distribution of foraminiferal genera

Across the platform, 22 foraminiferal genera examined here most commonly include miliolids, rotaliids, and textulariids (Fig. 2). The average abundance of foraminifera is 86 foraminifera/ml, and the average foraminiferal diversity index is 2.03, but both vary considerably. For example, genera diversity and abundance are highest nearer the shelf margin (back-reef shelf, southern unrimmed shelf and southern part of the shoal) (Table 3); the back-reef shelf has a Shannon-Wiener diversity index (H) of 2.23 and 175 foraminifera/ml, and the southern unrimmed shelf has an H =2.20 and 102 foraminifera/ml (Table 3). In contrast, geomorphic elements further from open-ocean conditions (northern part of the shoal, platform interior and the tidal flat) display lower diversity and foraminiferal abundances. For example, the northern part of the shoal has a diversity index (H) of 2.03 and the foraminiferal abundance (78 foraminifera/ml) lower than the platform average. The platform interior displays a slightly higher foraminiferal diversity (H = 2.05), but a slightly lower abundance (74 foraminifera/ml) than average. The tidal flat displays the most extreme values, with a diversity index of H = 1.57 and abundance of 55 foraminifera/ml. On CAP, the relative and absolute abundances of foraminiferal genera and water depth are uncorrelated (Fig. 3), perhaps because of the relatively limited range of depths on the platform top.

In general, the back-reef shelf area possesses foraminifera with the highest diversity and the highest absolute foraminiferal abundances. The second highest diversity and foraminiferal abundance occurs on the southern unrimmed shelf. The foraminifera of the platform interior and northern part of the shoal have comparable diversity, abundance and evenness. The tidal flat community has the lowest diversity and abundance of all geomorphic elements (Table 3).

In addition to the patterns of overall foraminiferal abundance and diversity, absolute and relative abundance of individual foraminiferal genera vary systematically across the CAP (Fig. 4 shows all data, Fig. 5 shows a representative transect across the platform). Some genera (e.g., *Archaias*, *Peneroples* and *Quinqueloculina*) are widespread across all geomorphic elements

(Fig. 4), although their abundance varies. *Archaias* commonly represents about 20 - 40% of foraminifera (Fig. 4a; Fig. 5). However, the abundance peaks (60%) in the platform interior just outboard of the tidal flat (where *Archaias* is absent) (Fig. 5). In contrast, *Peneroples* is common in tidal flat sediment, where it represents about 40% of the foraminifera. On the other geomorphic elements, *Peneroples* represents about 20%, except for the back-reef shelf, where the abundance is only about 7% (Fig. 4f; Fig. 5). Similarly, the highest abundance of *Quinqueloculina* is in the platform interior and the tidal flat, where it reaches up to 40% of the foraminifera. *Quinqueloculina* abundance is lowest on the back-reef shelf, where it reaches 5% in the area proximal to the barrier reef.

In contrast to these widespread genera, other foraminiferal genera are restricted spatially. *Astergerina* is most abundant (20%) on the outer shelf of the southern part of the platform (southern unrimmed shelf and southern part of the shoal), and is present (7%) on the back-reef shelf (Fig. 5). These geomorphic elements are dominated by coarse sediment (Table 2). Yet, this genus is absent in the platform interior and the tidal flat. Similarly, *Rosalina* occurs on the back-reef shelf, with abundance increasing up to 20% proximal to the barrier reef (Fig. 5), and is common on the ebb delta between Crooked Island and Long Cay. Encrusting foraminifera occur in highest abundance near reefs, especially the northern barrier reef (Fig. 4c; Fig. 5). *Homotrema* is abundant near the platform margin (back-reef shelf up to 35%, the southern unrimmed shelf up to 20%, southern part of the shoal up to 20%, and partially the northern part of the shoal up to 5%) (Fig. 4d; Fig. 5). These geomorphic elements are dominated by coarse sediment (Table 2). In contrast, *Textularia* is found in the platform interior and on the northern part of the shoal, where it averages about 10% of the foraminiferal community, and has a similar abundance in the back-reef shelf. *Textularia* is also present in the southern part of the shoal, although it averages only 4% of the foraminiferal community there. In the extreme, some foraminiferal genera are only present on one geomorphic element. For example, *Clavulina* is only abundant in the platform interior (< 15%) and on the northern part of the shoal (<5%) (Fig.

5), whereas *Milliolinella* dominates the foraminiferal community on the tidal flat (40%). These geomorphic elements are dominated by medium-sized sediment (Table 2).

Foraminiferal assemblages

The patterns of foraminiferal abundance and diversity across the platform can be captured statistically by Q-mode cluster analysis to characterize foraminiferal assemblages. Groupings based on the dendrogram with 40% similarity threshold (following the methods of Gischler et al., 2003) yields 8 assemblages (Fig. 6; Table 2). To test stability, cluster analysis can be run with only the most common foraminiferal genera, those with >10% abundance in at least one of the geomorphic elements (14 foraminiferal genera meet this criteria). The results with these 14 genera indicate that all 8 clusters are stable (assemblages are not driven by genera with small percentages, but the variations among the most common foraminiferal genera are large enough to differentiate the assemblages), which means that the most common foraminifera are driving these clusters. Only 6 samples (out of 181) were placed in different assemblages.

To better understand the relation between foraminiferal assemblages and the geomorphic elements, the assemblages, which are defined independent of the sample's location, can be compared to the geomorphic element from which they were collected (geomorphic elements interpreted independently by Rankey and Reeder, 2010) (Fig. 6 and 7). The results reveal that:

- Assemblage 1 (dominated by *Archaias*, *Quinqueloculina*, *Vertebrasigmoilina* and *Peneroples* (Fig. 6)) is distributed mainly in the platform interior and on the northern part of the shoal complex (Fig. 7; yellow circles). Two occurrences of assemblage 1 are present on the back-reef shelf, close to land.
- Assemblage 2 is distributed on the southern part of the shoal complex as well as much of the back-reef shelf (Fig. 7; red circles). The foraminiferal genera distribution between the southern part of the shoal and the back-reef shelf is different, however. The assemblage on the shoal is dominated by *Archaias*, *Homotrema*, *Quinqueloculina* and

Vertebrasigmoilina, whereas the assemblage on the back-reef shelf is dominated by *Archaias*, *Homotrema*, *Quinqueloculina* and *Rosalina* (Fig. 6). Based on these distinctions, the assemblage was split into two parts, assemblage 2s and 2b.

- Assemblage 3 includes mainly the foraminiferal genera *Archaias*, *Astergerina*, *Quinqueloculina* and *Vertebrasigmoilina* (Fig. 6). This assemblage has its main abundance on the southern unrimmed shelf, however, it is also present in the distal back-reef shelf close to land (Fig. 7; red circles).
- Assemblage 4 is represented almost entirely by *Archaias*, *Rosalina*, encrusting foraminifera and *Homotrema* (Fig. 6). Assemblage 4 is distributed in the proximal back-reef shelf close to the reef and in the tidal inlet close to the platform interior (Fig. 7; green circles).
- Assemblage 5 is composed mainly of *Laevipeneroples*, *Peneroples*, *Archaias* and *Quinqueloculina* (Fig. 6). This assemblage dominates the intertidal part of the tidal flat (Fig. 7; black circles).
- Assemblage 6 is dominated by *Quinqueloculina*, *Peneroples*, *Laevipeneroples* and *Articulina* (Fig. 6). This assemblage in present in only one sample in the intertidal part of the tidal flat (Fig. 7; yellow diamond).
- Assemblage 7 is composed mainly of *Quinqueloculina*, *Miliolinella*, *Articulina* and *Peneroples* (Fig. 6). This assemblage covers the supratidal section of the tidal flat (Fig. 7; red diamonds).
- Assemblage 8 is dominated by *Archaias*, *Rosalina*, *Articulina* and *Quinqueloculina* (Fig. 6). This assemblage is present in the ebb delta of the tidal inlet (Fig. 7; blue diamonds).

Note that the shoal includes two assemblages (assemblage 1 and 2s, yellow and red circles of Figs. 7a and 7b, respectively). Assemblage 1 occurs on the northern part of the shoal

complex up to the shoal crest, near the islands. Assemblage 2s covers the southern part of the shoal, oceanward of the islands. This foraminiferal differentiation is consistent with the observations of Rankey and Reeder (2010) and Rankey (2014), who noted that the southern part of the shoal includes coarser grains than the northern part of the shoal. The grain size difference was interpreted to be linked to different energy type and levels between shoal areas. In their interpretation, the southern area, facing the open ocean, has higher wave and tidal energy than the more protected, northern part of the shoal, which faces the platform interior. Based on these differences (in grain size, energy levels, and foraminiferal assemblage distribution) and to better assess both shoal areas, in this study, the shoal complex is divided into a southern part of the shoal and a northern part of the shoal with the subdivision at the shoal crest (area of shallowest water/ islands), roughly the position of the islands (dashed line in Fig. 7b).

Grouping by geomorphic element

ANOVA analysis provides a means to quantitatively test the significance of the differences in the variation of the mean of foraminiferal genus abundances among geomorphic elements. ANOVA analysis comparing the means of different genera among geomorphic elements reveals that the majority of genera have means that are distinct at the 95% significance (sig. values above 0.05). For example, *Clavulina* and *Rosalina,* present only on some geomorphic elements, have differences at the 99.5% significance level. In contrast, the genera *Archaias*, *Laevipeneroples* and *Vertebrasigmoilina* have a significance level above 0.05, and therefore have no different variance among the geomorphic elements at this significance level.

The analysis shows several trends. For example, between the northern part of the shoal and the platform interior, only two genera show different variance (Table 4). The second closest geomorphic elements are the southern part of the shoal and the back-reef shelf. Three genera have a different variance (Table 4). Between the southern part of the shoal and the northern

part of the shoal, six genera have a different variance (Table 4). The second most different geomorphic elements are the back-reef shelf and the platform interior as well as the northern part of the shoal. Nine foraminiferal genera have a different variance (Table 4). Between the southern part of the shoal and the platform interior only one genera is a similar variance (Table 4).

Although some foraminiferal genera do not have a different variance between some geomorphic elements, other genera do. Those foraminifera with different variances can be used to distinguish the geomorphic elements. Therefore, the whole foraminiferal community on each geomorphic element is distinct, and all geomorphic elements have a different distribution of the means of foraminiferal genera, at a 0.05 significance level. The two foraminiferal communities with the most similar distribution of the means are the platform interior and the northern part of the shoal.

ANOVA suggests that the communities of foraminiferal genera are statistically different among geomorphic elements. For comparison with ancient platforms, foraminifera here are compared on the family level due to extant species and evolved ecology of foraminifera (cf. Beavington-Penney and Racey, 2004). The major foraminiferal families on CAP are asterigerinidae (*Astergerina*), hauerinidae (*Quinqueloculina*, *Vertebrasigmoilina, Pyrgo, Miliolinella* and *Articulina*), peneroplidae (*Peneroples* and *Laevipeneroples*), homotrematidae (*Homotrema*), rosalinidae (*Rosalina*), soritidae (*Archaias*, *Cyclorbiculina* and *Sorites),* textulariidae (*Textularia*), valvulinidae (*Clavulina*). The family amphisteginidae (*Amphistegina*) does not exceed more than 2% in average foraminiferal communities, although amphisteginidae can have a higher abundance locally. Not surprisingly, like their component genera, foraminiferal families vary by geomorphic element as well (Fig. 8).

Foraminiferal trends through the Holocene

Foraminiferal distribution may change temporally, as geomorphic elements shift (e.g., through progradation or aggradation). To explore the Holocene stratigraphic record of CAP, foraminiferal characteristics in a prograding shoal complex (Rankey, 2014) and tidal flat system (Berkeley and Rankey, 2012) were analyzed.

Two 4.0 m-long (decompacted) cores, one from oceanward shoal complex (just south of the shoal crest) and one from interiorward (northern) shoal complex (close to the platform interior), provide insight into changes through time (Fig. 9a; red star). The relative abundances of different genera and the absolute abundances of foraminifera vary from the base to the top of cores and between cores (Fig. 9b, d). The Q-mode cluster analysis results for the foraminiefral core samples and the surface samples reveal that the oceanward (southern) core displays foraminiferal assemblages of the southern part of the shoal (Fig. 9c). The interiorward (northern) core contains only assemblage 1, which covers the platform interior and the northern part of the shoal (Fig. 9c).

Two (1.60 and 1.45 m-long) cores from the tidal flat include one from the present supratidal realm and one from the present intertidal realm (Fig. 9g; Berkeley and Rankey, 2012). The core from the supratidal realm (Fig. 9f) is dominated by *Miliolinella* (50-90%) with the highest abundance (70-90%) in between 82-136 cm depth of the core; *Quinqueloculina* (0-50%) has the lowest abundance around 100 cm depth. However, it is abundant (20-40%) above 109 cm depth, and at 163 cm, *Quinqueloculina* has a relative abundance of 50%. Additionally, *Peneroples* (0-10%) has a relatively constant abundance of ~ 6% in the upper half of the core (0-82 cm). The lower part has no *Peneroples*, except for the depth of 106 cm, which includes 10% *Peneroples*.

The core from the intertidal realm (Fig. 9h) also is dominated by *Miliolinella* (23-70%), with the lower part (104-145 cm) an abundance of 40-55%. The middle section (from 62-83 cm) includes about 30% *Miliolinella*, and the top 40 cm includes an abundance of *Miliolinella* (60-80 %). Foraminiferal distribution varies vertically as well. For example, in the lowest 20 cm

of the core, *Elphidium* reaches an abundance of 4% to 59% (this genus is absent on the modern platform) (Fig. 9h). Similarly, *Peneroples* (1-59%) and *Quinqueloculina* (3-51%) include their highest abundance in the middle section of the core. *Peneroples* generally is represented with an abundance of about 10%, but peaks (20-60% abundance) between 62-83 cm depth. Likewise, *Quinqueloculina* is not abundant near the bottom of the core, with only about 5% (at 144 cm). In contrast, in the interval between 83 and 124 cm, the abundance increases to around 50%. *Quinqueloculina* is most abundant with 20-30% in the top 62 cm of the core.

Comparing the foraminiferal distribution patterns in the tidal flat cores and the surface sediment samples using a Q-mode cluster analysis reveals that samples from most of both cores cluster with the modern supratidal samples (Fig. 9e; red diamonds). Only the middle sample of the intertidal core clusters with the modern intertidal foraminiferal community (Fig. 9h; black circle). Additionally, the lowest sample of the intertidal core forms a unique cluster by itself (Fig. 9h; blue circle), driven by the presence of *Elphidium*.

Discussion

Distribution of foraminiferal genera

As on other Caribbean platforms and reef systems, foraminiferal genera and abundance varies considerably across the area. Because larger benthic foraminiferal genera have different tolerances for environmental conditions (Murray, 1991), foraminifera are sensitive environmental indictors (Hallock and Glenn, 1986). On Crooked-Acklins Platform, individual genera of Holocene foraminifera illustrate distinct spatial distribution patterns that can be interpreted in the context of environmental preferences. Foraminiferal genera have different tolerances in terms of depth, energy conditions, salinity and temperature, and the requirements for substrates vary (Table 6).

In general, the distribution and abundance of foraminiferal genera vary across the platform; some are limited to one or a few geomorphic elements, and others suggest a specific geomorphic element by a higher or lower foraminiferal abundance than on other geomorphic elements. The

distribution of individual genera of foraminifera is linked to a range of factors, from salinity to bottom type to energy. Although some foraminiferal genera are indicative of specific geomorphic elements, a direct linkage of geomorphic elements to individual foraminiferal genera is ambiguous, as individual genera appear on a range of geomorphic elements.

Distribution of foraminiferal assemblages

Beyond the distribution of individual genera, the distribution of foraminiferal assemblages may be related to the geomorphic elements. In this study, analysis utilized a Q-mode cluster analysis to statistically define foraminiferal communities from all samples, independent of location (Fig. 6). A complimentary analysis grouped the foraminiferal communities by geomorphic elements, to analyze the characteristics of each geomorphic element (Table 5).

Q-mode cluster analysis revealed 8 assemblages (Fig. 6; Fig. 7) that collectively cover the different geomorphic elements. Assemblage 2 was divided into a shoal assemblage (2s) and a back-reef shelf (2b) assemblage, due to subtle differences in the foraminiferal genera. These different assemblages can be related to assemblages previously interpreted from other areas regionally, and interpreted in the context of energy, salinity, bottom type, circulation, and other environmental factors. The previously defined assemblages (Davis, 1964; Brasier, 1975; Hallock and Glenn, 1986; Murray, 1991; Gischler et al., 2003; Gischler and Möder, 2009) provided qualitative or quantitative descriptions of foraminifera, and form the basis for their assessment and interpretation in this study.

- Assemblage 1 (dominated by *Quinqueloculina*, *Archaias* and *Peneroples*) is the most widespread, covering most of the platform interior and the northern, northern part of the shoal complex, but it also occurs in the landward part of the back-reef shelf (Fig. 7; yellow circles). This assemblage appears broadly comparable to the *Archaias angulatus-Quinqueloculina-Triloculina* assemblage (Gischler et al., 2003) except that the CAP data include more *Textularia* and *Vertebrasigmoilina*.

- Assemblage 2b (dominated by *Archaias*, *Homotrema* and *Quinqueloculina*), which inhabits most of the back-reef shelf (Fig. 7; red circle). It can be described as a mix of Davis's (1964) leeward reef assemblages, with the addition of *Leavipeneroples*, *Homotrema* and encrusting foraminifera. However, assemblage 2b incorporates *Textularia*, which is only present in Davis's (1964) windward reef assemblage, an environment subject to higher energy.
- Assemblage 2s (dominated by *Homotrema*, *Archaias* and *Quinqueloculina*) inhabits the southern part of the shoal complex (Fig. 7; red circles). It can be compared to the sand blanket assemblage of Brasier (1975), which was described as occurring on unstable sediment consisting of recrystallized grains with ooids and peloids of Barbuda. However, the genera *Homotrema*, *Astergerina* and *Textularia* and encrusting foraminifera are not represented in Brasier's assemblage, so a direct comparison is ambiguous.
- Assemblage 3 is dominated by *Quinqueloculina*, *Astergerina*, *Homotrema* and *Vertebrasigmoilina*. It is present mainly on the southern parts of the southern unrimmed shelf on the southwest CAP, and in the back-reef shelf of northern CAP, proximal to land (Fig. 7; blue circles). This assemblage is analogous to *Archaias-Homotrema* assemblage (cf. Gischler and Möder, 2009) with the addition of *Vertebrasigmoilina*, *Articulina*, *Leavipeneroples* and encrusting foraminifera.
- Assemblage 4, with main components including encrusting foraminifera, *Archaias* and *Rosalina*, occurs on the outer parts the back-reef shelf (Fig. 7; green circles). This assemblage is most similar to the *Homotrema rubrum* assemblage (cf. Gischler et. al, 2003), with the addition of *Archaias*, *Rosalina* and encrusting foraminifera and with less *Homotrema*.
- Assemblage 5 (dominated by *Peneroples*, *Leavipeneroples* and *Quinqueloculina*) occurs only on the tidal flat, in the intertidal realm (Fig. 7; black circle). This

assemblage is comparable to *Quinqueloculina* assemblage of Murray (1991), although that assemblage lacks *Peneroples*.

- Assemblage 6 (dominated by *Quinqueloculina*, *Leavipeneroples* and *Peneroples*) is also found in intertidal settings (Fig. 9g; yellow diamond) (however, this assemblage is represented by only one sample). This assemblage is also similar to the *Quinqueloculina* assemblage (Murray, 1991), although the genera *Articulina* and *Peneroples* are not incorporated in the *Quinqueloculina* assemblage.
- Assemblage 7 is dominated by *Miliolinella*, *Quinqueloculina* and *Leavipeneroples*, and is most common in the supratidal realm (Fig. 7; red diamonds). This assemblage appears comparable to a mix of marine lagoon assemblage and hypersaline lagoon assemblage (Murray, 1991), except that the genus *Peneroples* is present in the CAP assemblage, but not in Murray's assemblages.
- Assemblage 8, dominated by *Archaias*, occurs almost exclusively in the tidal inlet (Fig. 7; blue diamonds). This assemblage is most similar to the windward reef assemblage of Davis (1964). However, *Rosalina* is present in assemblage 8 (illustrating proximity to reefs), but not in the windward reef assemblage of Davis (1964). Davis mentions high energy conditions and a high abundance of large foraminifera like *Archaias*; since *Rosalina* is smaller, it perhaps could have been transported away. Additionally, *Quinqueloculina* is not as dominant on CAP as it is in Davis's study area.

Geomorphic elements and foraminiferal assemblages have complicated relations. In some cases, two (or more) foraminiferal assemblages occur in one geomorphic elements. For example, the southern unrimmed shelf, southern part of the shoal and tidal flat are dominated by diverse conditions (Table 1). Due to the variable environments, the environmentally sensitive foraminiferal communities (Fig. 7) and the characteristic foraminifera (foraminiferal genus identifying a geomorphic element or a set of geomorphic elements) (Fig. 5 and 6) are

different across the geomorphic environment as well. For example, the back-reef shelf displays a transition from a high-energy reef environment of the barrier reef to a lower energy sediment-covered bottom close to land (Table 1). Conforming to these changing conditions, the foraminiferal assemblages vary as well (Fig. 5 and 7c). Overall, there are common foraminiferal trends (encrusting foraminifera, *Homotrema*, *Rosalina*, *Archaias* and a low abundance of *Peneroples*) (Fig. 5), but trends in the foraminiferal abundance, Shannon-Wiener diversity and Shannon evenness reveal a decrease with increasing distance from the margin (Table 3).

In other cases, the same assemblage can inhabit two geomorphic elements or parts of both geomorphic elements (e.g., platform interior and northern part of the shoal) (Fig. 7). In this latter situation, the platform interior and the northern part of the shoal probably display similar conditions (e.g., salinity and energy). The environmental similarity may drive the similar foraminiferal communities across boundaries between geomorphic elements (Hallock and Glenn, 1986; Murray, 1991).

These data, coupled with perspectives from other studies (Davis, 1964; Hottinger, 1983; Hallock and Glenn, 1986; Lidz and Rose, 1989; Murray, 1991; Gischler et al., 2003; Gischler and Möder, 2009), can be summarized in a schematic conceptual model for the nature and controls on spatial distribution of foraminifera across a Bahamian-type isolated platform (Fig.11). Energy level can be an important factor controlling foraminiferal distribution (Hottinger, 1983). Higher-energy geomorphic elements, especially those near the outer platform (Fig. 10), include robust foraminiferal genera (e.g., with thicker walls, forms such as *Astergerina*) and encrusting foraminifera (e.g., *Homotrema*) (e.g., Hallock and Glenn, 1986; Gischler et al., 2003; Gischler and Möder, 2009). Additionally, foraminiferal diversity and abundance is greater in these higher-energy areas (Fig. 10) (Gischler et al., 2003; Gischler and Möder, 2009). In quieter regions, such as the inner platform (Fig. 10), foraminifera usually

have thinner walls (Hallock and Glenn, 1986; Gischler et al., 2003), and foraminiferal diversity and abundance is lower (Fig. 10) (Gischler et al., 2003; Gischler and Möder, 2009).

Salinity influences the distribution of foraminifera (Hallock and Glenn, 1986). Generally, Bahamian isolated platforms include normal, open-marine salinity (Fig. 10 and Table 1) (Hallock and Glenn, 1986; Lidz and Rose, 1989; Gischler and Möder, 2009), although it may increase in restricted settings. For example, the tidal flat can vary in salinity from hypersaline to brackish, depending on precipitation and evaporation and winds (Fig. 10 and Table 1) (Lidz and Rose, 1986). Different foraminiferal suborders and genera have different tolerances for salinity (Hallock and Glenn, 1986; Murray, 1991). For example, rotaliines are tolerant to normal marine salinities. Miliolines (alveolinids, soritids, peneroplids, and miliolids) generally can tolerate higher salinities (Hallock and Glenn, 1986), and so can become dominant in these settings.

Another possible control on distribution is substrate. Bahamian-type isolated carbonate platforms can have diverse bottom types, from hardgrounds with corals and sponges, and coarse sediment on the open, outer platform, to medium and fine sediment with microbial mats and mangroves on the tidal flat (Fig. 10) (Davis, 1964; Hallock and Glenn, 1986; Lidz and Rose, 1989; Gischler et al., 2003; Gischler and Möder, 2009). Across this diversity, foraminiferal genera might be expected to vary, as some have different substrate requirements or preferences (Murray, 1991). For example, some foraminifera prefer to cling onto plants (e.g. *Peneroples*; Faber, 1991). Lidz and Rose (1986) indicate that *Archaias* prefers seagrass blades, or the sediment beneath them. Similarly, *Rosalina* prefers reefs (Lidz and Rose, 1989). Other genera require hardgrounds or at least larger rubble (e.g. encrusting foraminifera; Hallock and Glenn, 1986), or live free on the sediment (e.g. *Astergerina*; Lidz and Rose, 1989). A comparison of these bottom type preferences of the foraminiferal genera with the foraminiferal distribution of this study reveals similar trends (Fig. 10). However, on CAP *Archaias* is found also on sediment not associated with seagrass. The northern platform interior and parts of the back-

reef shelf are not populated by seagrass, but these areas are inhabited by *Archaias* (similar *Archaias* has been found on sediment by e.g. Write and Hay, 1971; Brasier, 1975; Hallock et. al., 1986).

Grain size is another possible influence for distribution of some foraminifera. Generally, the substrate, grain size of the sediment and vegetation play a role for the distribution of some foraminiferal genera (for more detailed information see Hottinger, 1983; Hallock and Glenn, 1986; Lidz and Rose, 1989; Murray, 1991; Beavington-Penney and Racey, 2004). For example, Hallock and Glenn (1986) indicate that miliolids, peneroplids, and small rotaliine prefer fine sediment. The distributions trends presented in this study are consistent with these distributions trends from the literature. Further, bioturbation and rhizoturbation provide a means of redistribution for organic matter, which can provide nutrients to the sediment-water interface. This change can favor the non-symbiont bearing foraminifera (Hottinger, 1983).

Turbidity usually plays a role for the foraminiferal distribution on the slopes carbonate platforms (Hottinger, 1983). However, in the shallow water of Bahamian platform tops, sunlight penetrates to the seafloor, so this control is probably not dominant.

Stratigraphic changes in foraminiferal assemblages

As geomorphic elements evolve through aggradation and progradation, the resultant stratigraphy records that history in the sediment, including the nature, abundance, and distribution of foraminifera. Analysis of sediment cores from the shoal and the tidal flat provides a means to assess how foraminiferal assemblages reflect the changes through time.

Comparing the foraminifera in the cores from the shoal to the surface sediment foraminifera reveals that the foraminifera of the oceanward (southern) part of shoal complex core resemble the modern assemblage 2s (which covers the southern shoal; Fig. 7) (Fig. 9c). In contrast, foraminifera in the platformward (northern) shoal complex core resemble surface-sediment

foraminiferal assemblage 1, which covers the platform interior and the platformward (northern) part of the shoal complex (Fig. 9g).

The modern foraminiferal assemblages of surface sediment differentiates between the two shoal parts, and these distinctions are evident in the assemblages through the cores of each flank. These temporally consistent foraminiferal abundance and assemblage patterns suggest that the foraminiferal differentiation present today across the shoal complex has persisted in this area throughout the Holocene record. That is, like the sedimentologic distinctions (Rankey and Reeder, 2011; Rankey, 2014), the foraminiferal differentiation between the northern and the southern shoal has remained consistent.

The foraminiferal assemblages do not reflect the change from platform interior deposits to shoal complex sediment, as interpreted (Rankey, 2014) from the sedimentology of the platformward core (Fig. 9c). Within cores, stratigraphic changes in the total abundance and in the abundances of individual foraminiferal genera suggest subtle changes, however. For example, differences in foraminiferal genera occur between the ooid-dominated section interpreted as shoal (0-120 cm; Rankey, 2014) and the bioturbated, peloid-dominated section interpreted as platform interior (160-240 cm; Rankey, 2014) (Fig. 9b, d). As an example, *Archaias* has a lower abundance (20-30%) in the lower (platform interior) sediment than in the upper (shoal) section (about 40%). This change may reflect the geomorphic transition, but in surface sediment, *Archaias* has an abundance between 25-40% in the northern part of the shoal and in the nearby platform interior. Comparably, although it is not dominant, the abundance of *Homotrema* is increased slightly, up to 1.2% (from 0.7% in the platform interior). This subtle increase is consistent with trends in surface sediment, and may reflect the greater open-ocean influence on the shoal. Nonetheless, other foraminiferal genera show no marked differences in distribution through the core. Thus, a correct interpretation of a comparable shoal system in the geologic record would require an integrated sedimentologic and foraminiferal

interpretation; use of foraminifera alone would not sufficiently differentiate geomorphic environments.

The tidal flat cores (Berkeley and Rankey, 2012) illustrate distinct sedimentologic patterns related to Holocene progradation of the tidal flat system (Fig. 9g). Comparison of assemblages defined from surface sediment and the foraminiferal assemblages in the cores do not include directly comparable patterns of assemblages (Fig. 9g). Instead, most of the samples from both cores (one from the supratidal realm (Fig. 9f), the other from the intertidal realm (Fig. 9h) cluster with the modern assemblage 7, which dominates surface-sediment samples from the supratidal realm. Importantly, however, this similarity is driven by the high abundance of *Miliolinella* in the cores (relative abundance between 30-90%); in the modern, this genus is only found in the supratidal realm, where it is has a high abundance, reflecting hypersaline conditions. *Miliolinella* aside, the other genera in the intertidal tidal flat core are more consistent with assemblage 5, which occurs in the present-day intertidal zone, than the assemblage 7, from the supratidal environment.

The occurrence of these "supratidal" foraminifera in the intertidal core is surprising, as the sedimentology suggests that this succession includes a transgressive deposit, overlain by a subtidal unit that shallowed to intertidal (Figure 9d; Berkeley and Rankey, 2011). Three possibilities may explain why this genus is present throughout the core. For one, *Miliolinella* could indicate episodes of hypersaline conditions in the intertidal domain that extended the habitat of *Miliolinella* into the intertidal realm. Another possibility for the appearance of this genus is storm surge retraction, which could carry *Miliolinella* from the supratidal down and out into the intertidal realm. A third possibility is that in these intertidal and subtidal sediments (Berkeley and Rankey, 2012) bioturbation or rhizoturbation re-distributed *Miliolinella* throughout the sediment column. These three possibilities are not mutually exclusive, and none can be definitively ruled out. Nonetheless, the results as a whole emphasize how considering assemblages alone may be somewhat misleading.

Another example is provided by the dominance of *Elphidium* at the bottom of the intertidal tidal flat core, in a zone interpreted as transgressive deposits (Berkeley and Rankey, 2012). This genus is not found in the modern surface sediment on CAP. *Elphidium* is generally found in the Bahamas on nearshore and lagoonal geomorphic elements, where it can tolerate salinities from hypersaline to brackish (Murray, 1991; Javaux and Scott, 2003). Due to the relatively thick shell, this genus also can withstand high energy conditions. These characteristics of *Elphidium* are consistent with the interpretation of Berkeley and Rankey (2012), that this interval represents high energy transgressive deposits.

Examining the foraminifera of the tidal flat core from the supratidal zone provides insight as well. The top 60 cm of that core includes a relatively homogeneous distribution of foraminifera (Fig. 9f). In contrast, the lower section (80-120 cm) has a more varied foraminiferal distribution (Fig.8 and 9d). In this section *Miliolinella*, *Peneroples* and *Quinqueloculina* have a greater range of relative abundances (Fig. 9f). This more varied and diverse fauna is consistent with the interpretation of these lower deposits as transgressive, subtidal, and intertidal sediment (Berkeley and Rankey 2012), distinct from the overlying sediment.

In general, a sedimentologic analysis should accompany the analysis of foraminiferal distributions. Both core sets from the shoal and the tidal flat show that the sedimentologic analysis defines the geomorphic elements better than the foraminiferal assemblages alone, but that foraminifera can provide additional insights.

Comparison of modern assemblages from CAP to ancient systems

Foraminifera in the stratigraphic record have been used to identify geomorphic elements, which commonly are interpreted to represent distinctive bathymetric, physical, and chemical environments. In many cases, studies of extant foraminiferal distribution are utilized as analogs

for environments in these ancient analogs. Benthic foraminifera that populate shallow marine environments are indicative of specific environmental conditions (e.g. Sun and Esteban, 1994; Geel, 2000; Wilson and Evans, 2002; Fournier et al., 2004; Daneshian and Dana, 2007). Although foraminiferal species and genera have gone extinct throughout the geologic record, foraminifera can still be interpreted through cautious use of the principal of taxonomic uniformitarianism, as informed by modern foraminiferal distribution studies (Hallock and Glenn, 1986; Beavington-Penney and Racey, 2004).

At a broad (family level) scale, foraminiferal distribution patterns on the Crooked-Acklins Platform are comparable with the patterns that have been described on ancient carbonate platforms, as illustrated by several examples:

- Many ancient *back-reef shelves* are characterized by encrusting foraminifera and rotaliines (homotrematidae, amphisteginidae, asterigerinidae and rosalinidae) (Fig. 8), as demonstrated by Miocene examples (Sun and Esteban, 1994; Büyükutku, 2003). These foraminifera are also characteristic of the back-reef shelf on CAP (Fig. 6).
- Some ancient *shelf assemblages* are inhabited by rotaliine (homotrematidae, amphisteginidae, asterigerinidae and rosalinidae) and textulariine (textulariidae) foraminifera (Pomar, 2001; Wilson and Evans, 2002). Although rotaliines contribute to the assemblage, textulariine are uncommon, representing only 2% of the modern foraminifera on CAP. Additionally, milioloids (hauerinidae) are the most abundant foraminiferal family in the modern foraminiferal group on CAP (Fig. 8). Another ancient example is the shelf assemblage represented in the Lower Red Formation (Oligocene, Central Iran), which is dominated by hauerinidae and some textulariidae and soritidae (Daneshien and Dana, 2007). Also, the overlying base of the Qom Formation is dominated by hauerinidae and some textulariidae, soritidae and asterigerinidae, which were interpreted to indicate a shelf as well (Daneshien and Dana, 2007).

- Several geologic *shoal complexes* include foraminiferal communities consisting of peneroplidae, soritidae and hauerinidae (Geel, 2000; Fournier et al., 2004). In the modern, both shoal foraminiferal communities (southern part and northern part of the shoal) are consistent with the ancient distribution.
- In some Oligocene and early Miocene *platform interiors*, foraminiferal assemblages consist of soritidae, rotaliines (homotrematidae, amphisteginidae, asterigerinidae and rosalinidae) and milioloids (hauerinidae) (Fournier et al., 2004). Although the general pattern is comparable, the modern sediment of CAP displays a higher relative abundance of peneroplidae in the platform interior than these ancient examples. This occurrence is reasonable, as the modern peneroplidae genera evolved during the Miocene (Loeblich and Tappan, 1988a). In the modern assemblage, alveolinids and rotaliines are very sparse (Fig. 8). Therefore, peneroplidae are more relatively abundant in the modern than in the ancient examples. Another ancient platform interior is a section of the Qom Formation (Rupelian–Burdigalian, Central Iran), which is dominated by hauerinidae, textulariidae, soritidae and peneroplidae (Daneshien and Dana, 2007). This section is overlain by strata displaying hauerinidae, textulariidae, soritidae, peneroplidae and valvulinidae (Daneshien and Dana, 2007), indicating an unrestricted platform interior.
- The Cenozoic model for the *restricted interior facies* (Hallock and Glenn, 1986) suggests that larger soritids and peneroplids are present. The dominant foraminifera, especially with increasing restriction, are miliolids (hauerinidae), due to their tolerance to higher salinities. This association corresponds very well with the trends on CAP. Studies of ancient platforms from the Oligocene (Fournier et al., 2004) and Miocene (Sun and Esteban 1994) show similar distribution of the foraminifera, including miliolids (hauerinidae) and peneroplids, along with low species diversity, in restricted marine settings. In the modern sediment of CAP, the tidal flat assemblage is characterized by an increasing relative abundance of miliolids (hauerinidae) towards the

supratidal. Peneroplidae are dominant in the subtidal and intertidal realms, but sharply decrease in abundance towards the supratidal (Fig. 8); few soritidae are present in the subtidal and intertidal.

Collectively, the trends in foraminiferal distribution found on the Crooked-Acklins Platform are broadly comparable to the distribution patterns present in numerous ancient carbonate platforms. Even though foraminiferal distribution patterns and geomorphic elements are linked (Hallock and Glenn, 1986; Gischler and Möder, 2009), few studies of ancient analogs utilize foraminifera as indicators for geomorphic elements. Although the Crooked-Acklins platform may not be a perfect analog for all systems, the results of this study provide an actualistic, conceptual model for constraining spatial heterogeneity and geomorphic patterns that may be present in ancient analogs.

Conclusions

This study statistically explored the linkage of geomorphic elements and foraminiferal assemblages through analysis of foraminiferal abundance and diversity data from Holocene sediment of Crooked-Acklins Platform of the southern Bahamas. Understanding the foraminiferal distribution patterns in connection with the geomorphic elements on this modern isolated carbonate platform provides insights that could be used for understanding and predicting spatial heterogeneity and geomorphic patterns in ancient analogs.

The results reveal trends in foraminiferal distribution patterns. The geomorphic elements are inhabited by a range of foraminiferal communities. These foraminiferal communities are composed of generalists (*Archaias*, *Peneroples* and *Quinqueloculina*), which are present across the isolated carbonate platform, and specialists (such as *Clavulina*, *Miliolinella* and *Astergerina*), which occur on only one or few geomorphic elements. Likewise, the diversity and abundance of individual foraminiferal genera varies systematically across the isolated carbonate platform. The geomorphic elements closer to the open ocean (back-reef shelf,

southern unrimmed shelf, and southern part of the shoal) have a higher foraminiferal diversity and foraminiferal abundance. The geomorphic elements in the platform (northern part of the shoal, platform interior and tidal flat) have a lower foraminiferal diversity and foraminiferal abundance (the intertidal realm, marked by a high foraminiferal abundance, is an exception).

In the shallow subsurface, in areas with few taphonomic alterations, foraminiferal assemblages can distinguish geomorphic elements, if the foraminiferal communities are distinct. In areas with taphonomic alteration, the foraminiferal genera distributions and foraminiferal abundance can provide insight into the succession of geomorphic element. Nonetheless, coupled sedimentologic and foraminiferal data provide the most complete interpretation.

In general, the results illustrate characteristic differences in foraminiferal abundance, diversity and assemblages among most geomorphic elements. The results provide a conceptual model that may aid the understanding of the distribution spatial variability of geomorphic elements or respective facies bodies on modern and ancient analogs (e.g. Arun gas field in northern Sumatra; Asmari Formation in Iran and the Qom Formation in central Iran).

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Figures

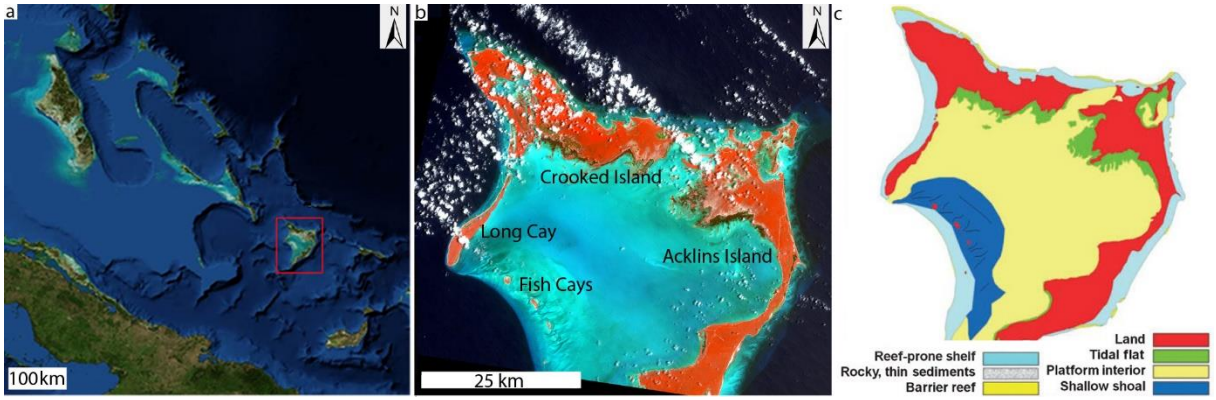

Fig. 1: Location and geomorphology of Crooked-Acklins Platform (CAP). a: Regional setting, with red box indicating location of CAP in the southeastern part of the Bahamian archipelago. b: Landsat image of CAP. Note the shallow platform interior surrounded by islands on three sides, and a shoal complex ("Fish Cays") on the south/southwestern side. c: Interpretation of geomorphic elements (modified from Rankey and Reeder, 2010). Note the distribution and spatial relationships of the geomorphic elements. The tidal flat fringes the southern parts of Crooked Island and Acklins Island. The shoal complex is a barrier between the southern unrimmed shelf and the platform interior. The reef in the north is continuous and is flanked to the south by a 1-3 km wide back-reef shelf.

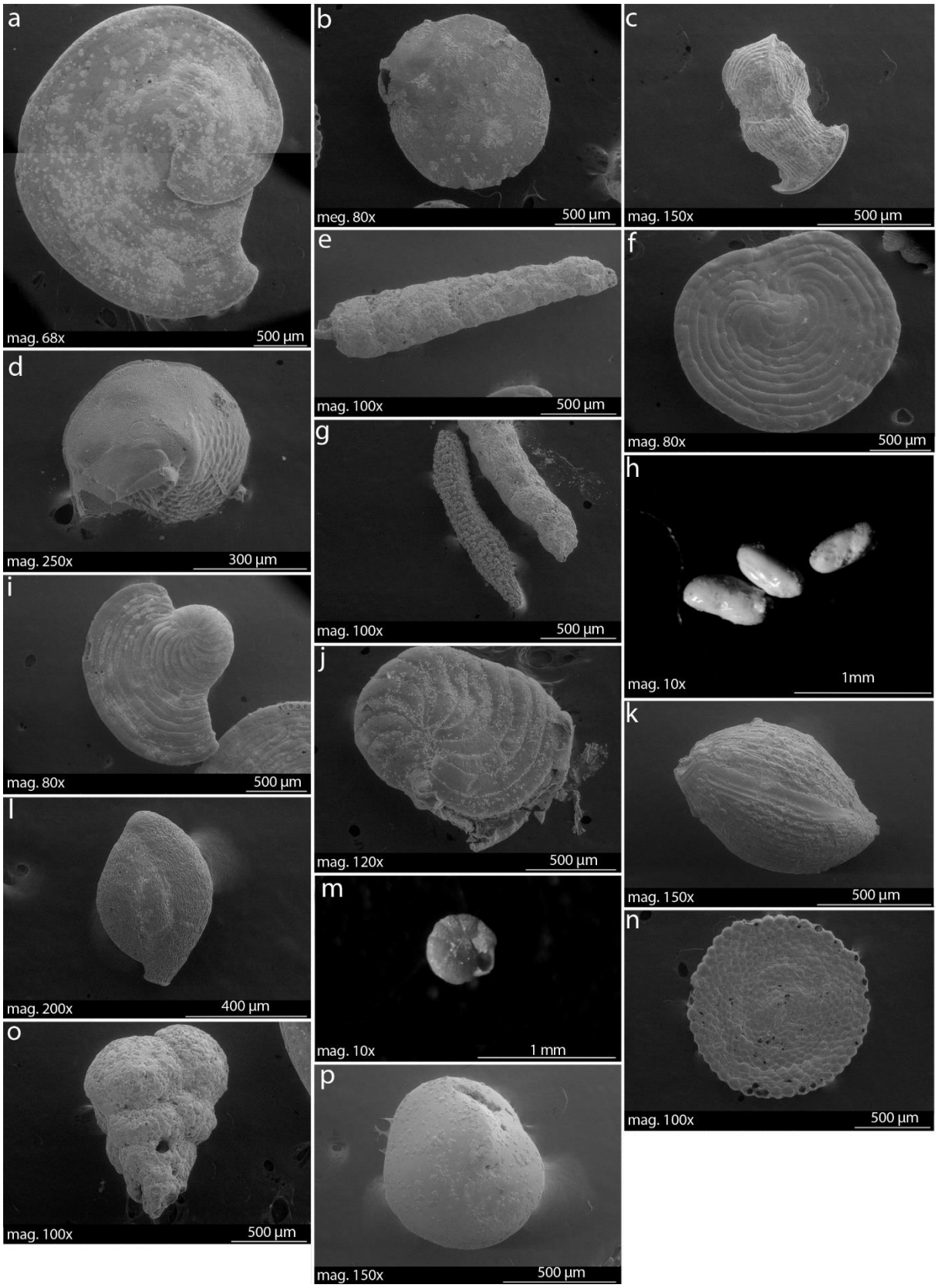

Fig. 2: SEM images and photomicrographs of representative foraminiferal genera. a) *Archaias*, b) *Amphistegina*, c) *Articulina*, d) *Astergerina*, e) *Clavulina*, f) *Cyclorbiculina*, g) *Homotrema*, h) *Miliolinella*, i) *Laevipeneroples*, j) *Peneroples*, k) *Pyrgo*, l) *Quinqueloculina*, m) *Rosalina*, n) *Sorites*, o) *Textularia*, p) *Vertebrasigmoilina*.

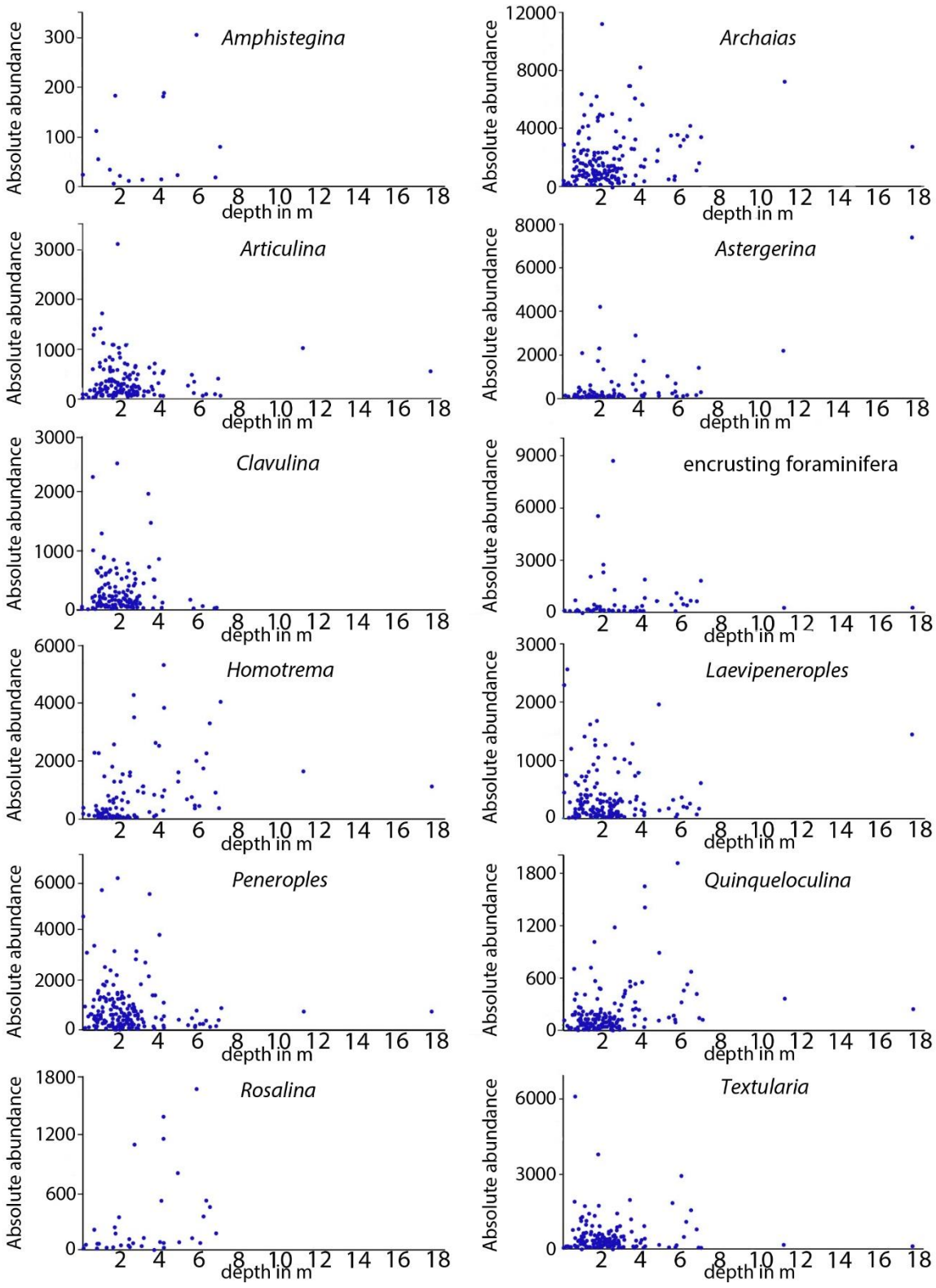

Fig. 3: Abundance of representative foraminifera genera (plotted as absolute abundance; foraminifera / 10ml sediment) as a function of water depth. Note that there are no pronounced changes in abundance of foraminifera genera with depth on this platform.

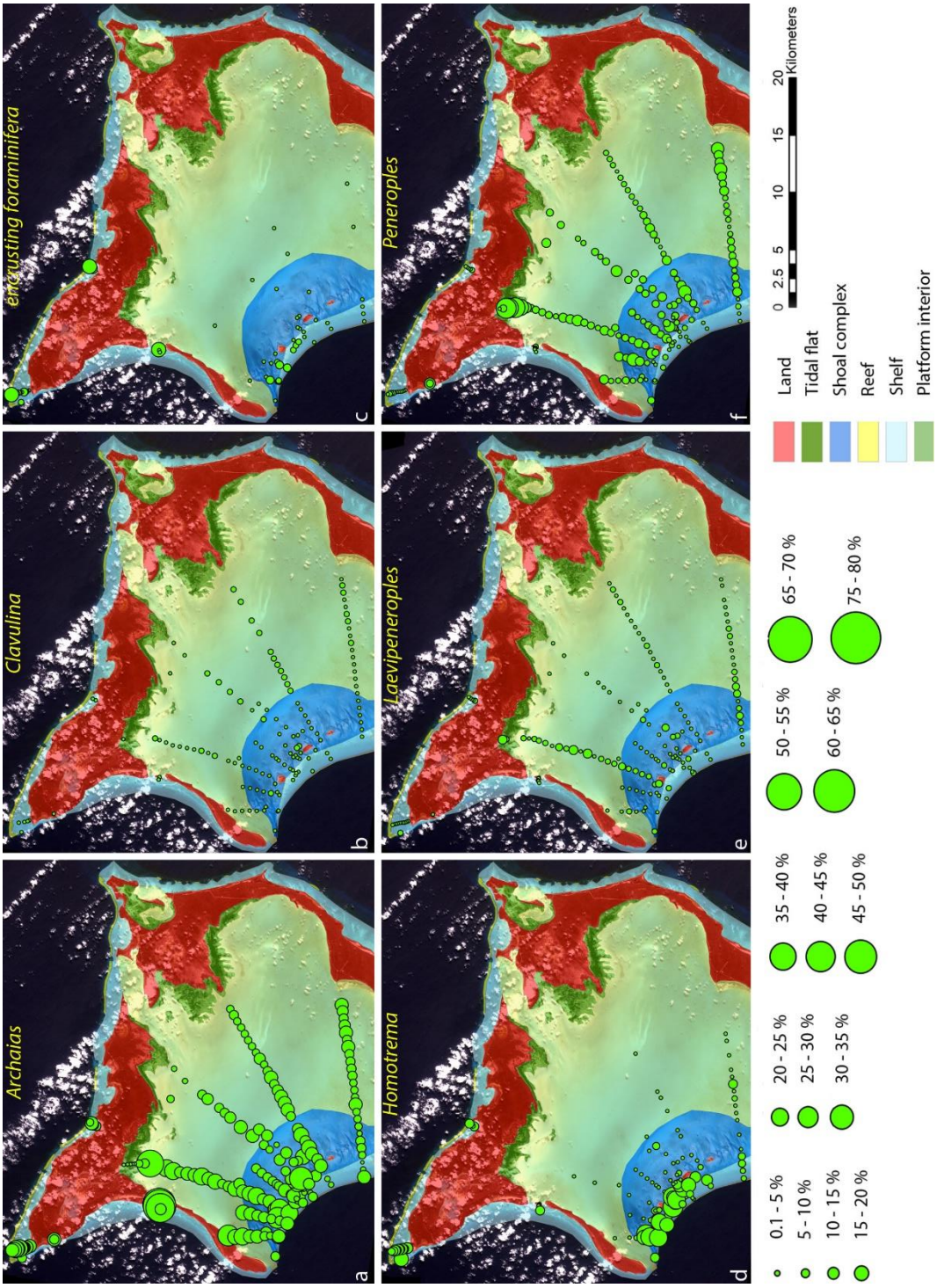

Fig. 4: Spatial patterns in relative abundance of illustrative foraminiferal genera. Some foraminiferal genera (a: *Archaias*, f: *Peneroplis*, e: *Leavipeneroplis*) are widespread across the platform, whereas others (b: *Clavulina*, c: encrusting foraminifera, d: *Homotrema*) have a more restricted distribution.

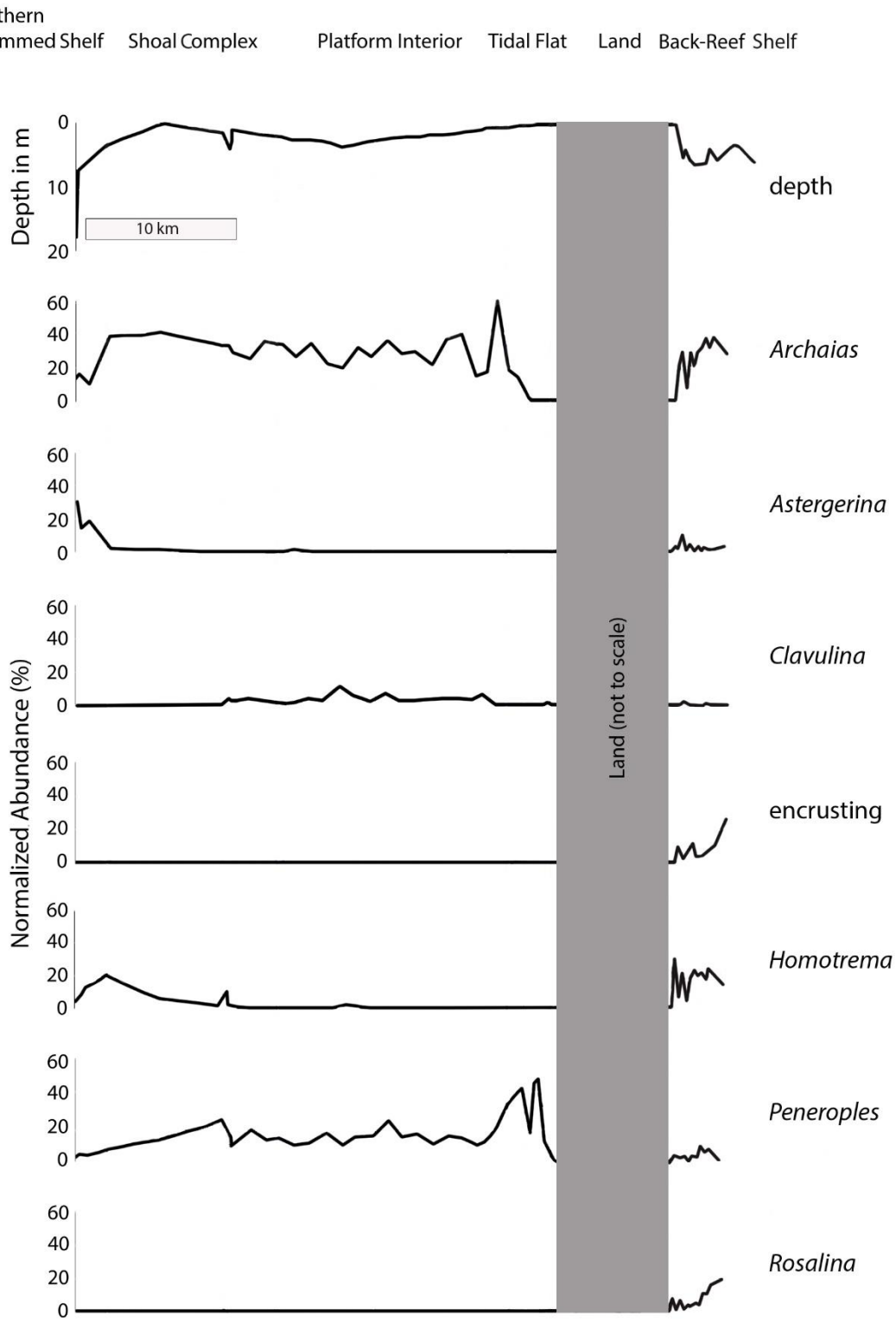

Fig. 5: Relative abundance of foraminiferal genera along a representative transect across CAP (combining the westernmost transect and across the back-reef shelf, Fig 2). Note the different distributions of various genera. Some (e.g. *Peneroples*) are present across the platform, albeit with varying abundance. Others are distributed across the platform except in certain areas (e.g., *Archaias* is absent in tidal flat sediment*)* and others (e.g. *Astergerina*, *Homotrema* and *Rosalina*) inhabit specific geomorphic elements or groups of geomorphologic elements.

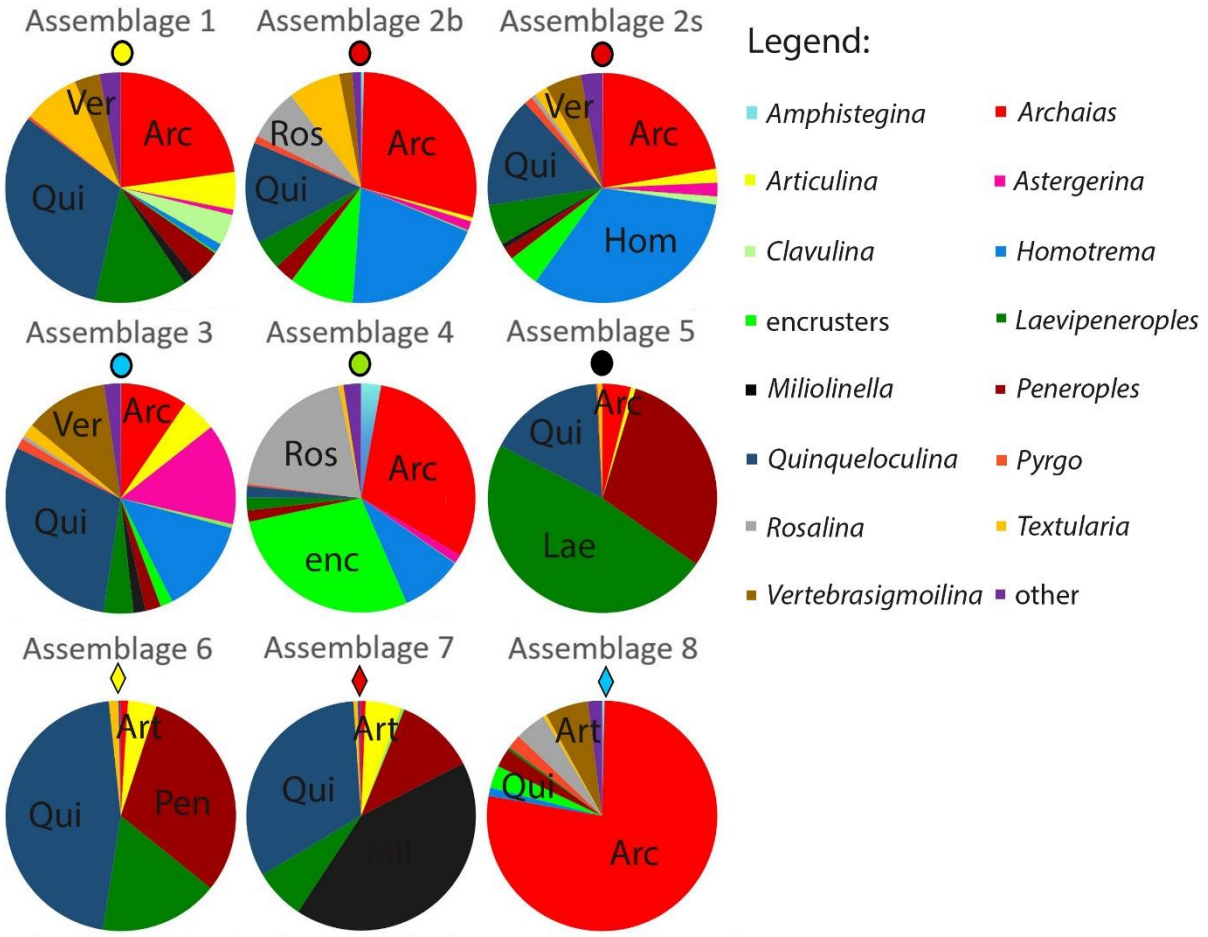

Fig. 6: Pie chart representation of composition of foraminiferal assemblages (defined by Q-Mode cluster analysis) expressed as relative abundance of the genera in each assemblage. To help highlight distinctions, three genera characteristic of each assemblage are labelled in each chart (Arc = *Archaias*; Art = *Articulina*; enc = encrusting foraminifera; Hom = *Homotrema*; Mil = *Miliolinella*; Lae = *Laevipeneroples*; Pen = *Peneroples*; Qui = *Quinqueloculina*; Ros = *Rosalina*; Ver = *Vertebrasigmoilina*). Assemblage symbols above each pie correspond to those used in Figs. 4, 5, and 10. Note the different proportions of the genera among assemblages and distinct foraminiferal genera in assemblages.

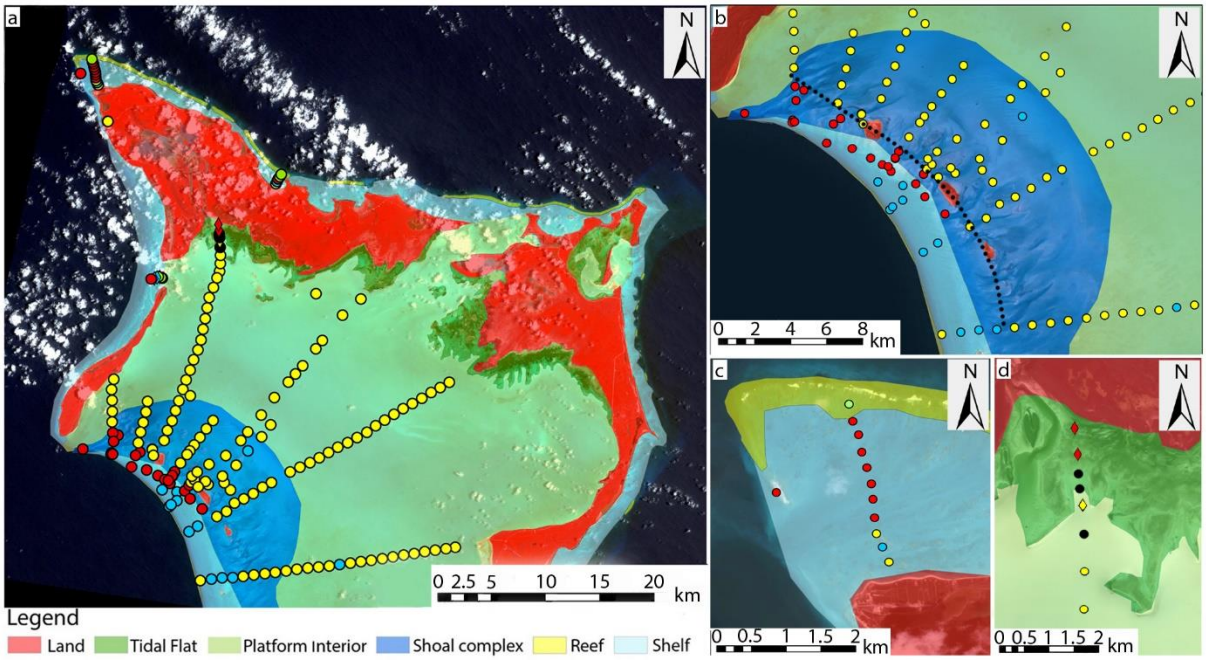

Fig. 7: Spatial distribution of foraminiferal assemblages (symbols correspond with Fig. 6) across the platform, co-plotted with geomorphic elements (interpretation of Rankey and Reeder 2010). a: the entire platform. b: Detail of the shoal complex. c: Detail of the northern back-reef shelf. d: Zoom of the tidal flat. Note how the distribution of the foraminiferal assemblages corresponds in most cases to the geomorphic elements. Some geomorphic elements include more than one assemblage; for example, the back-reef shelf has 4 foraminiferal assemblages, and the tidal flat incorporates 3 assemblages. In contrast, some assemblages span across two geomorphic elements. For example, the platform interior and the northern part of the shoal complex are inhabited by the same foraminiferal assemblage, and the southern part of the shoal complex is distinct.

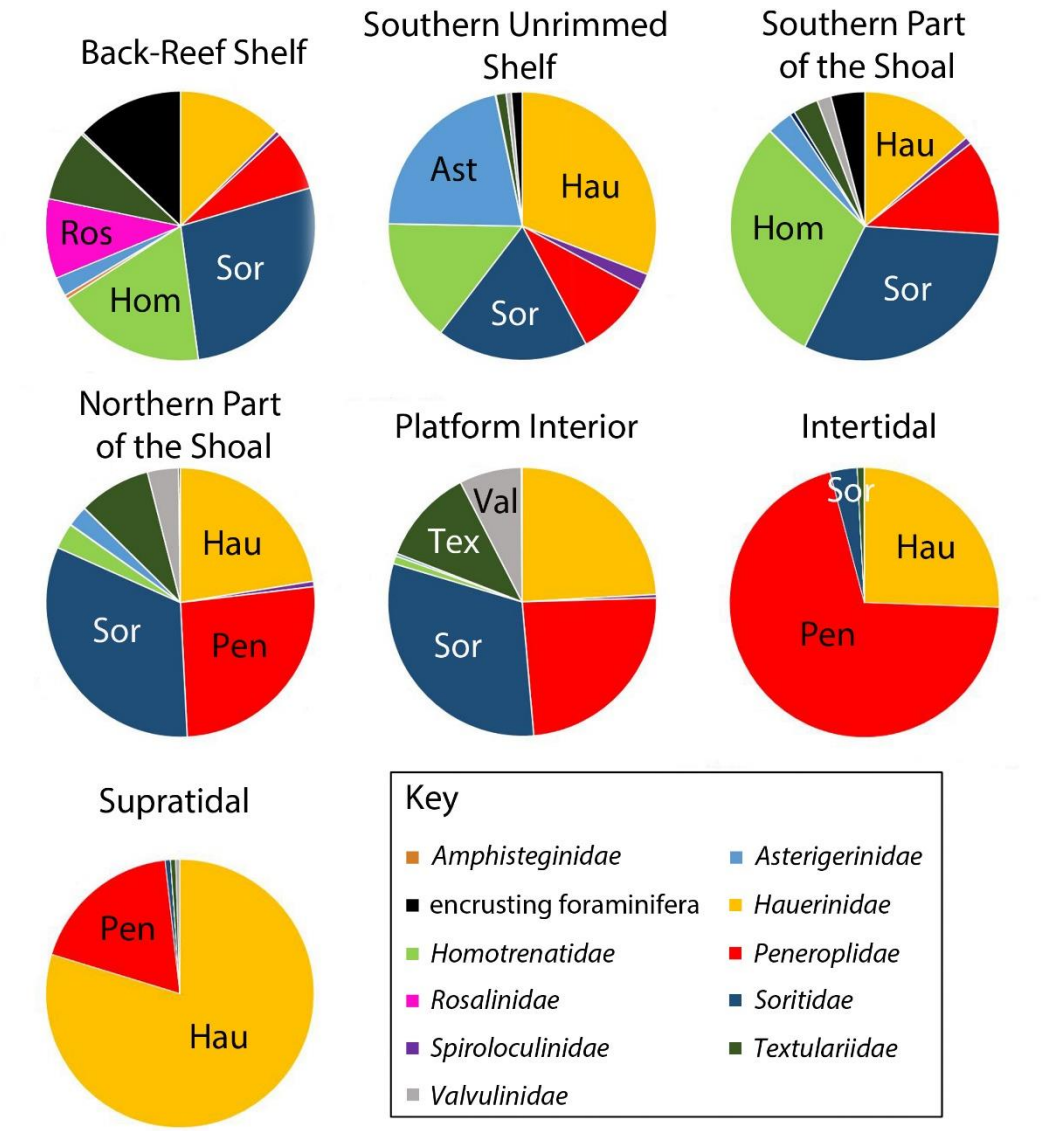

Fig. 8: Composition of the mean abundance of foraminiferal families within each geomorphic element. Note the shift from dominance by homotrenatidae, soritdae, hauerinidae and peneroplidae on the outer platform (southern unrimmed shelf, back-reef shelf and southern part of the shoal) to common soritidae, peneroplidae and textulariidae on the inner platform (northern part of the shoal and platform interior) to hauerinidae and peneroplidae on the tidal flat. Additionally, three families characteristic of each element are labelled in each chart for more explicit distinctions (Ast = asterigerinidae; Hau = hauerinidae; Hom = homotrenatidae; Pen = peneroplidae; Ros = rosalinidae; Sor = soritidae; Tex = textulariidae; Val = valvulinidae).

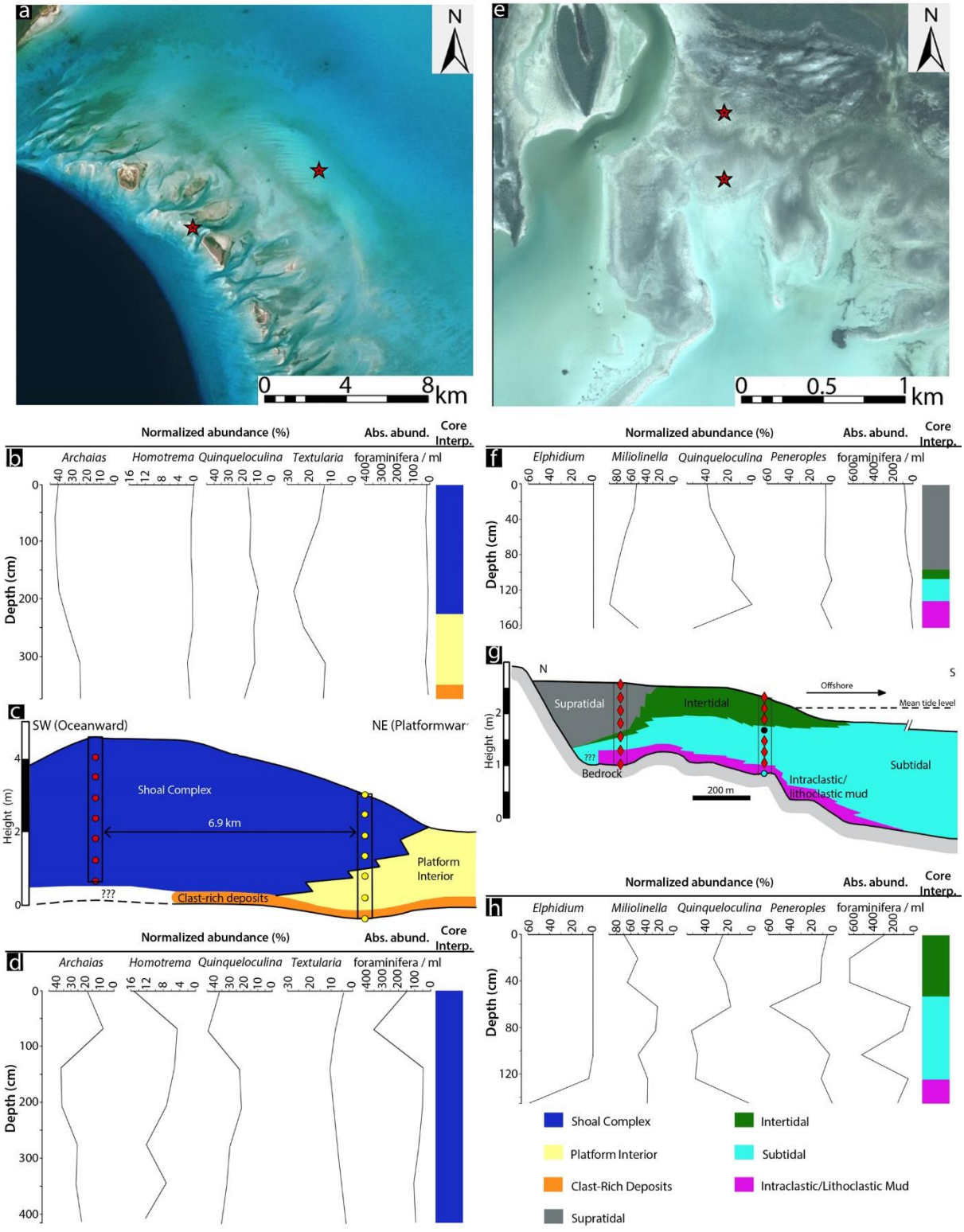

Fig. 9: Distribution of foraminifer in cores. Location of shallow sediment cores from the shoal complex (a) and the tidal flat (e) (red stars). Distribution of selected foraminifera from the northern part of the shoal core (b), the southern part of the shoal core (d), the supratidal core (f) and the intertidal core (h) in normalized abundance (in percent, defined as number of specimens of a genus divided by the total number of specimens). c: Foraminiferal assemblages from the core samples, superimposed a sedimentologic interpretation (Rankey, 2014), which

suggested the platformward progradation of the shoal complex. Note the core from the southern part of the shoal displays only the 2s assemblage (red circles in a) and the core from the northern part of the shoal displays only the assemblage 1, consistent with the surface sediment in the area of the cores. g: Location of shallow sediment cores from the tidal flat (red stars). Note the core from the supratidal and the intertidal display mostly the assemblage 7. Only one sample from the intertidal belongs to the assemblage 5 and the oldest sample in this core does not cluster with any modern clusters. The dominance of assemblage 7 indicates that clusters are not a useful tool to analyze this facies body. Note the transitions of the changes of the foraminiferal abundances with the interpreted geomorphic elements.

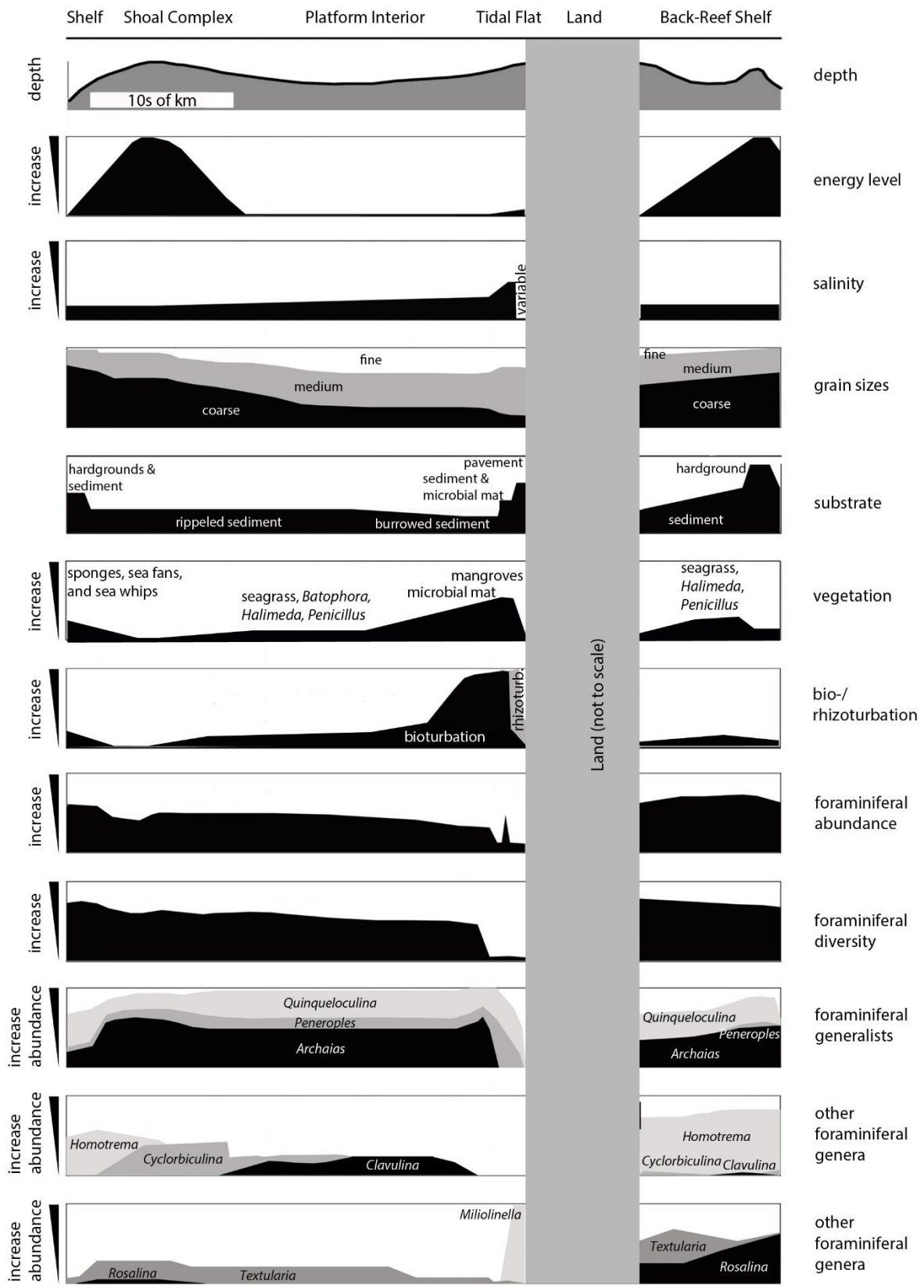

Fig. 10: Conceptual model of the linkages among environmental variables, geomorphic elements, and foraminiferal communities on a Bahamian-type isolated carbonate platform.

Geomorphic element	Tidal energy	Wave energy	Salinity	Water depth	Bottom types	Epifauna
Back-reef shelf	Low	High	Normal marine	3- 7 m	Rocky to reefal bottom. Towards the island, sediment cover is more common	From reef coral, seafans and seawhips (oceanward) transitioning to seagrass, *Halimeda*, *Penicillus* (landward)
Tidal inlet, including ebb delta	High: strong currents	Low	Normal marine	1.5- 5 m	Stabilized dunes and ripples transitioning shelfward to active ripples. Inlet includes rocky to coral- or red algal-covered bottom. Seagrass beds locally.	Varying (dense to none) seagrass, sponges, red algae, *Batophora*, *Halimeda*, *Penicillus*, corals, and sparse burrows
Tidal flat	Low	Low	Hypersaline, variable with occasional fresh water	< 1 m	Highly variable, but mostly bare sediment to microbial mat cover. Supratidal hardground	Dense mangrove vegetation in intertidal, and bare supratidal
Platform interior	Medium	Low	Normal marine	1- 3 m	Stabilized to active ripples, locally bioturbated	Varying cover of seagrass, sponges, *Batophora*, *Halimeda*, *Penicillus*, corals, and burrows
Shoal	High	Low, except at flanks	Normal marine	< 3 m	Stabilized to active ripples, locally bioturbated	Varying cover of sponges, seagrass, *Penicillus*, *Halimeda*, *Manicina*, and *Batophora*
Southern unrimmed shelf	Low	High	Normal marine	>3m	Active to stabilized ripples, bioturbated sand, small patch reefs, rocky bottom	Varying cover of coral, sponges, sea fans and sea whips
Western leeward shelf	Low	Moderate	Normal marine	0 to >5m	Active to stabilized ripples, bioturbated sand, rocky bottoms, local patch reefs	Varying cover of corals, sea fans and sea whips, seagrass, *Halimeda* and *Penicillus*

Table 1: Summary of general environmental setting and characteristics of geomorphic environments on Crooked-Acklins Platform. Information from Rankey and Reeder (2010), Berkeley and Rankey (2012), Rankey (2014) and field observations.

	Southern unrimmed shelf	Southern part of the shoal	Northern part of the shoal	Platform interior	Tidal flat	Back-reef shelf
Characteristic Foraminifera	*Articulina*, *Astergerina*, *Rosalina*, *Homotrema*, *Vertebrasigmoilina*	*Cyclorbiculina* (<10%), *Pyrgo*	*Clavulina*, *Cyclorbiculina* (10%)	*Articulina*, *Clavulina*, *Cyclorbiculina* (5%)	*Miliolinella*	*Encrusting foraminifera*, *Rosalina*, *Homotrema*
Generalist	*Archaias* (<20%), absence of *Textularia*	*Quinqueloculina* (<15%)	*Quinqueloculina* (<15%)	*Quinqueloculina* (20-40%)	absence of *Archaias*, *Laevipeneroples* (20-40%), *Peneroples* (40%)	*Textularia* (20%)
% silt and clay (<63µm)	0.2	0.6	1.7	2.0	3.3	0.3
% Medium and fine sand (63µm to 500µm)	21.5	43.7	55.8	67.6	67.4	31.4
% Coarse sand & coarser (>500µm)	77.4	54.8	41.0	29.4	28.8	67.8
Visual estimation of bioturbation	<10%	<10%	<10%	5-90%	90-95%	<10%
Sediment	Medium sand; skeletal fragments composite grains and peloids	Coarse to fine sand; ooids and peloids	Medium to fine sand; ooids and peloids	Fine sand; peloids, skeletal fragments	Muddy fine sand; peloids, gastropod shells	Gravelly medium sand; peloids and coral fragments
Equivalent Dunham texture	Skeletal grainstone	Ooid grainstone	Ooid grainstone	Peloid-skeletal grainstone	Packstone	Coral-peloid grainstone to Boundstone

Table 2: General sedimentologic attributes and foraminiferal genera associated with geomorphic elements. Note that the geomorphic elements with coarser sediment (southern unrimmed shelf and back-reef shelf) are inhabited by similar foraminiferal genera. The geomorphic elements with more abundant fine to medium fraction (e.g., the northern part of the shoal and the platform interior) have similar foraminiferal genera. The tidal flat is populated by a distinct foraminiferal population.

	Southern unrimmed shelf	Southern part of the shoal	Northern part of the shoal	Platform interior	Tidal flat	Back-reef shelf
Shannon-Wiener diversity (H)	2.20	2.12	2.03	2.05	1.57	2.23
Shannon evenness (E)	0.71	0.67	0.65	0.67	0.63	0.71
Abundance (foraminifera/ ml)	102	62	78	74	55	175
Number of samples	10	30	43	73	5	17

Table 3: Shannon-Wiener diversity (H), Shannon evenness (E), and foraminiferal abundance in the sediment of distinct geomorphic elements. The H, E and abundance are highest on geomorphic elements nearer the margins of the platform (back-reef shelf, southern unrimmed shelf and southern part of the shoal) and decrease into the platform interior (northern part of the shoal, platform interior and tidal flat).

Geomorp. element	Compared to geomorp. element	*Articulina*	*Astergerina*	*Clavulina*	*Cyclorbicul-ina*	Encrusting foraminifera	*Homotrema*	*Peneroples*	*Pyrgo*	*Quinqueloc-ulina*	*Rosalina*	*Textularia*
Southern shoal	Northern shoal	0.025	**0.768**	0.041	**0.949**	0.000	0.000	**0.255**	**0.367**	0.000	0.003	**0.093**
	Platform interior	0.021	0.000	0.032	**0.558**	0.000	0.000	0.028	0.008	0.005	0.001	0.017
	Back-reef shelf	**0.426**	**0.778**	**0.056**	0.006	0.000	**0.806**	**0.055**	**0.954**	**1.000**	0.000	**0.104**
Northern shoal	Platform interior	**1.000**	0.008	**1.000**	**0.866**	**0.943**	0.000	**0.750**	**0.345**	**0.105**	**0.962**	**0.907**
	Back-reef shelf	0.000	**0.230**	0.000	0.028	0.000	0.000	0.000	**0.147**	0.000	0.000	**1.000**
Platform interior	Back-reef shelf	0.000	0.000	0.000	**0.156**	0.000	0.000	0.000	0.002	0.006	0.000	**0.886**

Table 4: Matrix of significance values of ANOVA correlations of foraminiferal abundance between sets of geomorphic elements. [Note the tidal flat and the shelf are not included due to the small sample size. Additionally, *Archaias*, *Laevipeneroples* and *Vertebrasigmoilina* show no significant variation among the geomorphic elements and therefore excluded.] These values are used in the ANOVA analysis to determine if a foraminiferal genera has a significant variance between two geomorphic elements. The geomorphic element in the first column is compared to the one in the second column. Values above 0.05 (values above that indicate similar variances of the foraminiferal genus in both geomorphic elements) are highlighted in bold. In general, in a comparison between the geomorphic elements, the more values above 0.05 for the genera, the more similar the foraminiferal communities are.

	Southern unrimmed shelf	Southern part of the shoal	Northern part of the shoal	Platform interior	Tidal flat	Back-reef shelf
Amphistegina	0	0-1	0-1	0	0	0-3
Archaias	5-26	6-55	4-36	8-60	0-1	7-37
Articulina	2-9	0-9	0-10	0-21	1-7	0-4
Astergerina	2-31	0-23	0-17	0-9	0	0-9
Clavulina	0-3	0-5	0-8	0-14	0-1	0-1
Cyclorbiculina	0-4	0-9	0-10	0-9	0	0-2
Encrusting foraminifera	0-3	0-15	0-2	0-2	0	3-34
Homorema	4-24	0-47	0-13	0-15	0	4-30
Laevipeneroples	0-7	0-11	0-14	0-24	6-40	0-7
Miliolinella	0	0	0	0	0-51	0
Peneroples	2-12	0-22	3-27	5-45	1-50	0-9
Pyrgo	0-2	0-7	0-3	0-5	0-1	0-2
Quinqueloculina	0-5	0-10	1-13	0-36	0-1	0-37
Rosalina	0	0-4	0-1	0	0	0-33
Sorites	0-1	0-3	0	0	0	0-1
Textularia	0-2	0-9	0-19	0-35	0-1	0-30
Verterbrasigmoilina	2-37	0-17	0-18	0-20	0	0-13

Table 5: Ranges of relative abundances of foraminiferal genera among geomorphic elements. Note some foraminiferal genera are present on all geomorphic elements (*Archaias*,

Peneroples and *Quinqueloculina*). Other genera (e.g. *Miliolinella*, *Clavulina* and *Sorites*) are only present on some geomorphic elements.

Table 6: General environmental conditions that favor selected foraminiferal genera. Note

	Energy tolerance	Salinity	Temperature	Depth	Substrate	Areas on CAP	References
Archaias	High – low	32-37 °/oo	22-33°C	< 20m	Lives on plants and sediment	Southern unrimmed shelf, shoal complex, platform interior, back-reef shelf	Hallock et al., 1986; Lidz and Rose, 1989; Murray, 1991; Gischler et al., 2003
Peneroples	High – low	35-53 °/oo	18-27 °C	< 70m	Plants, sediment, hard grounds	Northern shoal, platform interior and tidal flat, less abundant on southern unrimmed shelf, back reef shelf and southern shoal	Hallock, 1984; Lidz and Rose, 1989; Culver, 1990; Faber, 1991; Murray, 1991
Quinqueloculina	High – low	32-65 °/oo	Cold to warm	< 100m	Plants, sediment	Higher abundance in platform interior tidal flat and back-reef shelf; lower in shoal complex and southern unrimmed shelf	Lidz and Rose, 1989; Murray, 1991; Javaux and Scott, 2003
Textularia	High – low	Normal marine	Cold to warm	< 500m	Hard grounds, plants, sediment	Back-reef shelf, platform interior, shoal complex	Lidz and Rose, 1989; Murray, 1991; Javaux and Scott, 2003
Miliolinella	High – low	Hypersaline to brackish	10-30 °C	< 100m	Hard substrates	Supratidal realm	Loeblich and Tappan, 1988a, Lidz and Rose, 1989; Murray, 1991
Clavulina	Moderate to low	Normal marine		< 30 m	Sediment	Platform interior and the northern shoal and back-reef shelf	Lidz and Rose, 1989; Javaux and Scott, 2003
Astergerina	High	Normal marine	Subtropical-tropical	Shallow water	Sediment and plants	southern unrimmed shelf and back-reef shelf close to the island	Lidz and Rose, 1989; Murray, 1991; Javaux and Scott, 2003
Rosalina	High – low	Normal marine	Temperate to warm	< 100m	Hard substrates (e.g. corals, plants)	ebb delta on the western shelf and back-reef shelf; absent on southern unrimmed shelf,	Lidz and Rose, 1989; Murray, 1991; Javaux and Scott, 2003
Homotrema	Very high	Normal marine	Temperate to warm	Shallow water	coarse sediment, hardgrounds, corals and reefs.	southern unrimmed shelf and northern back-reef shelf	Loeblich and Tappan, 1988a; Murray, 1991; Javaux and Scott, 2003; Gischler and Möder, 2009
Encrusting foraminifera	High to medium	Normal marine			hard substrates	near reefs (back-reef shelf, western shelf)	Brasier, 1975; Gischler et al., 2003; Gischler and Möder, 2009

Archaias, *Peneroples* and *Quinqueloculina* have high tolerances and are present on most geomorphic elements on CAP. The other genera have more specific requirements (e.g. *Astergerina*) than these first three generalist genera. Broad tolerance ranges, not shared by other genera, allows some foraminifera genera (e.g. *Miliolinella*) to thrive in settings where other genera are not present.